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NATURAL HISTORY
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ZOOGEOGRAPHY OF THE
LAND AND FRESH-WATER MOLLUSCA
OF THE NEW HEBRIDES

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Zoogeography of the Land and Fresh-Water Mollusca of the New Hebrides¹

INTRODUCTION

Zoogeography attempts first to describe, then to interpret, the present distribution of animal life. The development of descriptive zoogeography has been well summarized by Schmidt (1954, 1955), and a modern synthesis of classical descriptive vertebrate geography has been presented by Darlington (1957).² Basing their work primarily on the study of birds and mammals, with some data derived from the cold-blooded vertebrates, biologists have divided the world into a series of faunal "realms, regions, and provinces." The exact number of the various units and the boundaries between them are subject to individual appraisal, and much of the zoogeographical literature is concerned with the delineation of faunal regions.

In recent years there has been a change from pure descriptive zoogeography to an analysis of the ecological bases for animal distribution and a discussion of the historical phenomena responsible for the faunas of today. The problems of environmental geography and its zoogeographical import have been summarized by Hesse, Allee, and Schmidt (1951). There is no similar source on historical zoogeography, although much information is contained in G. G. Simpson (1953a,b) and Darlington (1957).

Classical zoogeography deals with the distribution of animal life at a given time in the earth's history. For any group of organisms, there is no question that "the present distribution . . . is due to (1) the geological history of the area; (2) its palaeo-climatic history; (3) the rate of evolution in the group; and (4) the mode and rate of dispersal in the group." (Uvarov *in* Scrivenor et al., 1943, p. 165.) The relative importance of these factors varies with each taxon and

¹ Modified from a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the University of Michigan, 1956. A brief summary of this report has been published (Solem, 1958c).

² This work appeared some eight months after the completion of my manuscript. While a few minor factual changes have been made on the basis of information offered by Darlington, my thesis is essentially the same, and only a few cross references have been inserted below.

many of the discrepancies between the biogeographic schemes proposed for different animal or plant taxa are the result of such variations.

This study considers the present distribution of the Pacific Ocean land snails. Darlington (1957) summarized the distribution of the non-marine vertebrates. The patterns shown by the land snails and the non-marine vertebrates are not the same, and I have not tried to fit the land snails into the pattern of vertebrate geography. The static (present) zoogeography of the two taxa is different, I believe, because they are not equally able to cross the filter zones created by physical and climatic barriers.

In discussing the origin of a biota, it is necessary to consider all the organisms that inhabit the area, but limitations of time and knowledge have prevented my making more than a cursory attempt to integrate knowledge about other animals and plants into a comprehensive theory of the origins of the Pacific land biota. Some information on the vertebrates, insects, and vascular plants has been incorporated, but most of the data comes from the distribution and geological history of the land snails.

As background information for the descriptive zoogeography and hypothetical origin of the fauna, I have included brief statements on geology and zoogeography, the phylogeny of the land snails, the age of the land Mollusca, and the dispersal of island-dwelling organisms.

Prior studies on Pacific land snail distribution have been based on the Polynesian fauna (Pilsbry, 1900b, 1916, 1921; C. M. Cooke, 1926; Crampton, 1916, 1925, 1932; Germain, 1932, 1934; and H. B. Baker, 1941). Hedley (1892a, 1899) considered Melanesia and New Zealand, Iredale (1937a) Australia, and Tera van Benthem Jutting and Ilse and Bernhard Rensch provided many data on Indonesia and northern Melanesia. The New Hebrides contain land snails derived from all parts of the Pacific region and thus serve as a good focal point from which to undertake a synthesis of the information on distribution. Careful comparisons have here been made between the New Hebridean species and those of Australia, New Caledonia, northern Melanesia, Polynesia, Micronesia, and New Zealand. Lack of time, material, and comprehensive systematic reviews has prevented my making more than the most generalized survey of the Indonesian fauna. The information obtained from these comparisons is summarized in the discussion of faunal shifts (pp. 295-296) and the detailed discussions of particular areas (pp. 296-305) that precede the delineation of zoogeographic areas that are based on land snail distribution.

GEOLOGY AND ZOOGEOGRAPHY

If we temporarily ignore chronological differences in time of spread, it should be possible to utilize the same basic theory of geology to explain the distribution of all living organisms. Unfortunately, three completely different geological theories have been widely quoted (see Just, 1947):

- (1) That the present continental shelves have existed throughout geological time.
- (2) That numerous trans-ocean land bridges have been created between continents.
- (3) That there has been "continental drift" (Wegener's hypothesis).

The permanence of continents has been championed by most vertebrate zoologists from Darwin and Wallace to the present day (see Schmidt, 1955, pp. 771, 777-781). Few would challenge the statement that the distribution of the living vertebrates can be readily explained without invoking any radical changes in the position and size of the continental shelves.

Most of the advocates of trans-ocean land bridges have been students of the fauna and flora of the southern hemisphere. Similarities between the vertebrates of South Africa, South America, New Zealand, and Australia are comparatively few, but there are striking resemblances between many of the invertebrate and plant taxa of those areas. The disjunctive southern distributions have led many observers to propose trans-ocean land bridges or to suggest that Antarctica may have been a migration route (see also p. 317). Every square foot of ocean bottom has been covered by a land bridge proposed to explain unusual distributions. As a natural reaction to the gross misuse of "land bridges," it has become suspect to propose any alterations in present land areas other than a few hundred feet of change in sea level during the last glaciation.

An alternative to the building of land bridges was presented by Wegener's hypothesis of "continental drift." Briefly, this theory assumes that the continents were formerly united into a single land mass, became fragmented, and drifted to their present positions. Although this has been used to explain disjunctive southern distributions (for example, Good, 1953), and many geologists favor the theory, I can find no evidence in land snail distributions which can be more easily explained by "continental drift" than by the permanence of continents. Bucher (1952, p. 101) reviewed the geological evidence on continental drift and concluded that "the concept of

continental drift cannot be used as a working hypothesis by the student of animal and plant distribution." In this paper no further reference has been made to this theory.

Study of the geology of the Pacific region is greatly handicapped by the comparatively small amount of land area and the great extent of the ocean. Most of the islands are composed of coral limestone and volcanic rocks and have only limited surface features available for study. Soundings have revealed the presence of numerous flat-topped "guyots" scattered throughout the central Pacific, and the deep core drillings in the Marshall Islands (see pp. 19-20) have produced very important data on the probable history of the area. Ladd (1957, 1958) reported evidence from pollen samples and fossil land snails (see also p. 255) that shows Bikini was formerly a "high island" at least as large as some of the smaller Hawaiian islands of today. The large amount of limestone rock underneath both Bikini and Eniwetok is conclusive evidence that the ocean floor has subsided during the Tertiary Period at least 4500 feet. No geological evidence is available for the Melanesian area, but the biological evidence presented below suggests that there have been important changes in land area in this region.

The Tertiary subsidence of Micronesia helps to reconcile the differences between the vertebrate zoologists (Mayr, 1940a, b, 1953a; Myers, 1951, 1953a, b; and Darlington, 1948, 1957), who considered the Pacific islands to have an "oceanic" fauna, and the malacologists (Hedley, 1892a, 1899; Pilsbry, 1900b, 1916, 1921; Crampton, 1916, 1925, 1932; C. M. Cooke, 1926; and Germain, 1932, 1934), who considered that at least part of the fauna was derived via "land bridges." While there probably never was a "continental mass" in the Micronesian area, there almost certainly were many more "high" islands than there are today, and thus the distances between islands were much less. This hypothesis and that of the *earlier* arrival of the land snail fauna (see pp. 318, 320, 323) explains the simultaneous existence of the primitive, relict land snail fauna and the modern vertebrate fauna.

In the Melanesian region, changes of one or two thousand feet in elevation on the New Hebrides (see p. 19, no. 1, this volume) have occurred since the Miocene, while New Caledonia and New Zealand have a very long and complex history of elevation and subsidence. The faunal evidence presented in the following sections suggests that parts of the land snail and vertebrate faunas were isolated in the Mesozoic. The hypothesis that these original elements were derived over a more or less continuous "land bridge" is without direct

geological evidence but seems to be supported by data drawn from several groups of animals and plants.

While only geological studies will prove or disprove this hypothesis, the geological changes suggested would date prior to the last great period of mountain building and would require elevation of existing submarine mountain ridges rather than change in major contours. This possibility, though it differs from much modern zoogeographical theory, clarifies the many unusual features of the distributions of Pacific land snails.

PHYLOGENY OF THE LAND SNAILS

Gastropods have made the transition from aquatic to terrestrial life several times and "land snails" consist of several phylogenetic elements. Discussion of the affinities of the different lineages is well beyond the scope of this study. The most recent survey (Boettger, 1954) reviews the higher euthyneuran (opisthobranch and pulmonate) categories and presents a "family tree" (op. cit., p. 263). Utilization of the Euthyneura-Streptoneura or Prosobranchia-Opisthobranchia-Pulmonata divisions does not alter the basic multiple origin of land snails. Perhaps five major groups (fig. 10) produced land mollusks: the Systellommatophora, Basommatophora, and Stylommatophora (collectively termed the Pulmonata), and two prosobranch orders, the Archaeogastropoda and the Mesogastropoda. In the Mesogastropoda, the land snails come from several different marine ancestors.

Within the dominant Stylommatophora, there have been four or five radiations (fig. 11), indicated by the Heterurethra, the Tracheopulmonata, the Orthurethra, the Mesurethra, and the Sigmurethra. The Orthurethra, probably the most primitive, occur today as minute species on the continents (Pupillidae, Valloniidae) or as secondarily enlarged dominant species on oceanic islands (Partulidae, Achatinellidae). The Heterurethra (Succineidae) and Tracheopulmonata (Athoracophoridae) are closely related (Boettger, 1954, p. 271, and H. B. Baker, 1955, p. 109) and perhaps should be united into the Elasmognatha. The Mesurethra (Corillidae, Cerionidae, Acavidae) are a few relict families found in widely scattered regions of the world. By far the greatest number of species belong to the Sigmurethra.

The relative number of species in each of these categories varies from region to region (fig. 9). The Systellommatophora, Tracheopulmonata, Heterurethra, and Basommatophora are represented by few species. The Archaeogastropoda are important only in the

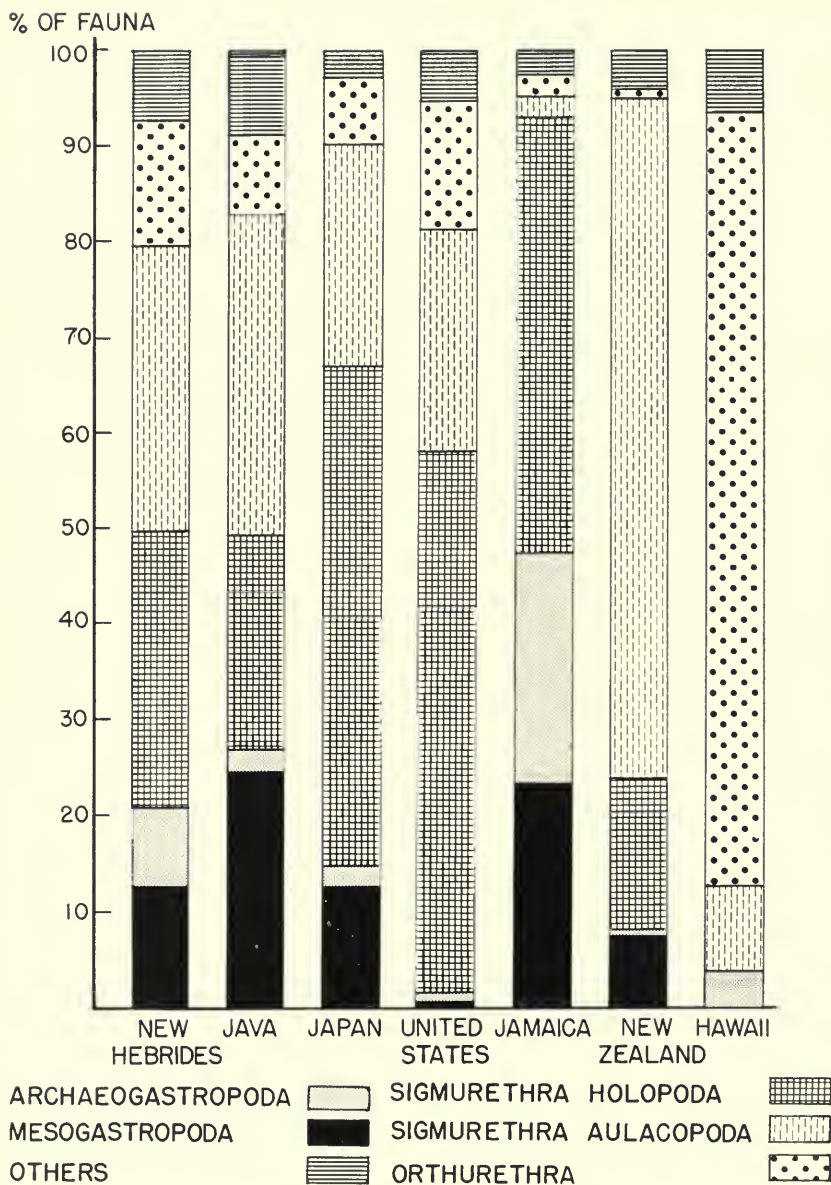


FIG. 9. Proportionate representation of land snail orders in different faunas. The Mesurethra are not represented in the areas listed, with the exception of one species of *Cerion* (out of more than 700 species) in the United States.

Greater Antilles. The Mesogastropoda are insignificant in the United States, but important in some island regions. The Orthurethra and Sigmurethra (Holopoda and Aulacopoda) form the dominant elements in nearly every region. Unfortunately, many areas of the world are too poorly known to allow any sweeping conclusions as to group distribution and importance at this time.

The phylogenetic relationships of the major pulmonate categories are very uncertain. Pilsbry (1900b, p. 570) implied that the Heterurethra and Sigmurethra are separate developments from the Orthurethra, but H. B. Baker (1955) suggested that the ancestral Sigmurethra were both heterurethrous and aulacopod. Further than these suggestions, no information is available.

Based on data given in the systematic review (No. 1, this volume), the possible phylogenetic relationships of the land mollusks are presented (figs. 10 and 11). The diagrams are based on the studies of Pilsbry, H. B. Baker, Hugh Watson, and Thiele, and they show the diverse origins of the land snails. It would be presumptuous to indicate affinities between the major divisions of the Stylommatophora (fig. 11) or the major gastropod categories (fig. 10), and the sub-units are represented as independent lines arising from the major category. For many families and superfamilies more definite conclusions can be drawn. Connecting lines indicate relatively certain affinities, dotted lines and question marks those of increasing uncertainty.

Many of my conclusions are tentative and few other malacologists will completely agree with the proposed system, although much of it may be generally accepted. This is the first attempt to present a "family tree" of the Stylommatophora since that of Pilsbry (1900a, p. 564) and, despite imperfections, it can at least form a basis for modification by other workers.

On the evidence of anatomical structure, the Partulidae, Paryphantidae, and Endodontidae seem to be the most primitive members of their suprafamilial categories. Together with the Bulimulidae, they form the dominant members of the New Hebridean fauna.

The land snails probably underwent rapid adaptive radiation and most of the major categories must have appeared in a relatively short time. The continental Orthurethra and Heterurethra have survived because of their occupation of limited ecologic niches that have been ignored by the more progressive Sigmurethra (Pilsbry, 1916, p. 430). The disjunctive distribution, few species, and varied shell morphology all suggest that the Mesurethra are relicts now in

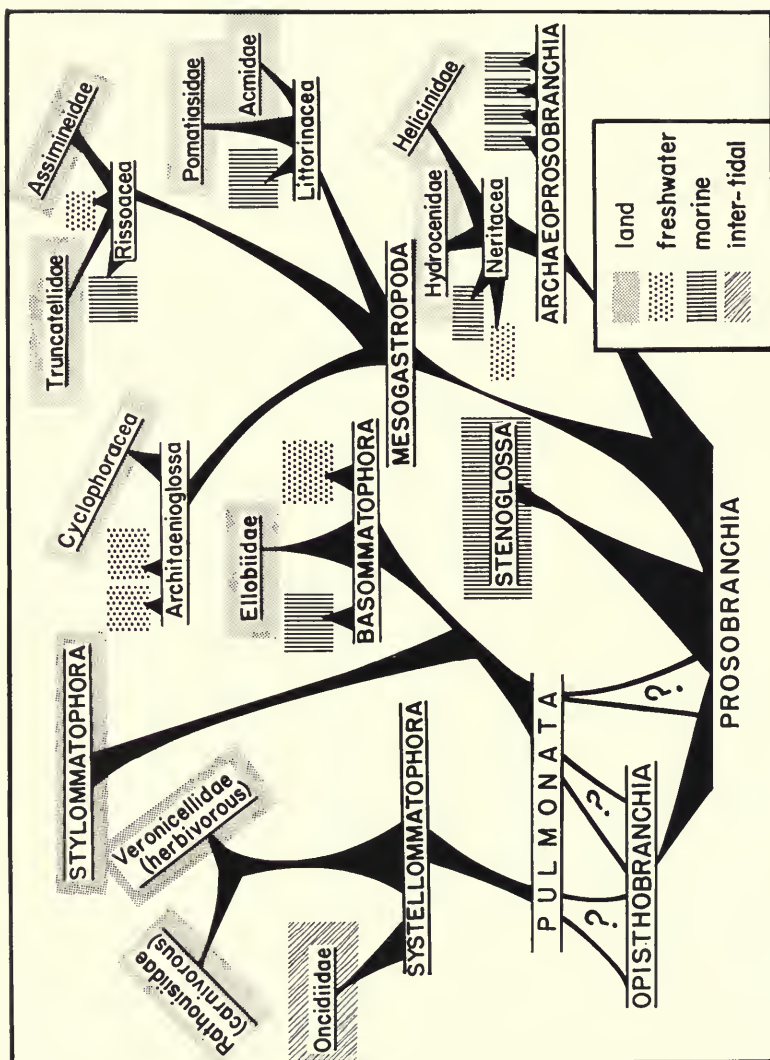


FIG. 10. Phylogeny of land Mollusca.

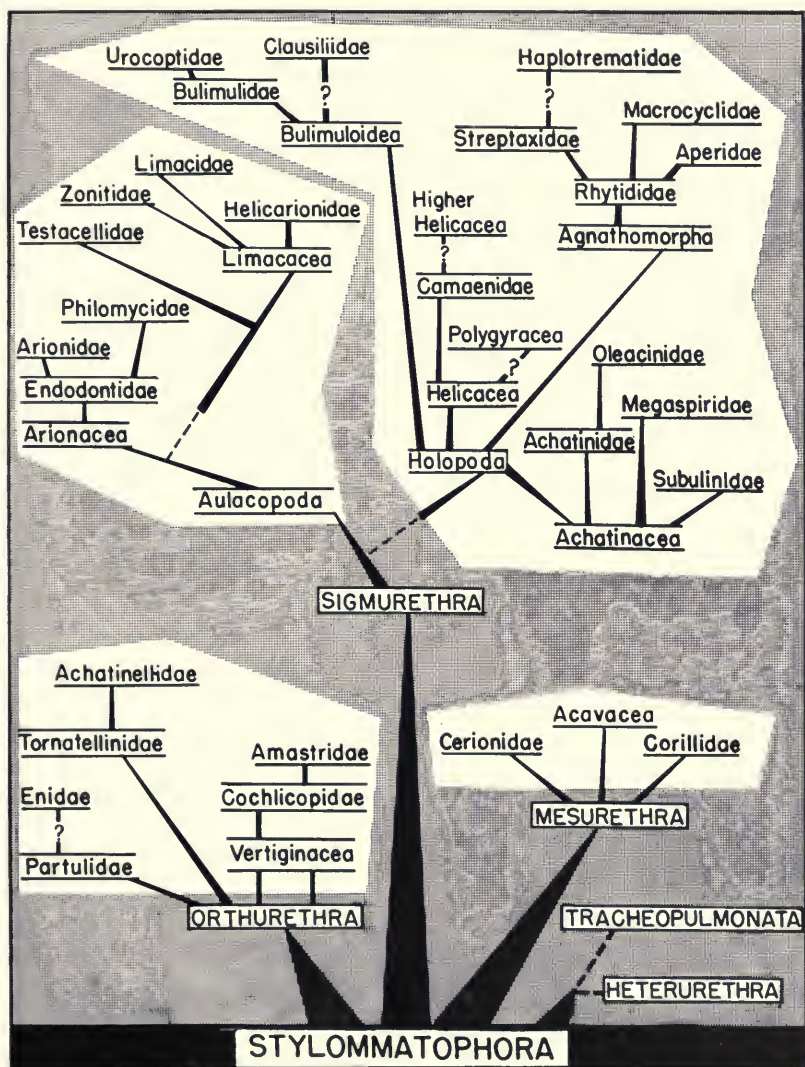


FIG. 11. Phylogeny of Stylommatophora.

the process of being replaced by the Sigmurethra. Evolution has of course proceeded within each category and several sigmurethran families found in the New Hebrides are replaced by other families in most continental areas. On the major continents the Streptaxidae replace the Paryphantidae, and in the Holarctic the Limacacea the Endodontidae, and possibly the Helicacea the Bulimulidae.

The above information emphasizes the primitive nature of the New Hebridean land snail fauna. Acceptance of this conflicts with the modern character of the vertebrate fauna (pp. 311-316) of the New Hebrides. This places that fauna in the same category as those of New Caledonia, Australia, and New Zealand, all of which are characterized by a great number of "living fossils" and relative paucity of advanced taxa.

AGE OF THE LAND MOLLUSCA

Information on the geologic age of the land mollusks is very scarce. Many marine shells are known from Mesozoic and Paleozoic strata, but there are comparatively few authenticated records for pre-Tertiary land and fresh-water snails. This scarcity is probably caused by many factors. Areas of fresh-water fossil deposition are small in comparison with marine zones and generally are more likely to be exposed to subsequent erosion. The shell of marine mollusks is composed of calcite, which is readily preserved, while non-marine mollusks have shells of aragonite, which is much less permanent.

The earliest land snail fossils are found in the Pennsylvanian formations of Illinois, Ohio, New Brunswick, and Nova Scotia. Included are a helicid(?), *Dawsonella*; a helicoid snail similar to the endodontid *Discus*; and several "pupillids" of uncertain affinities (see Pilsbry, 1926, pp. 316-319, pl. 32, and Wenz, 1938-44, pp. 52-56). Regardless of whether the "pupillids" are Ellobiidae, Pupillidae, Cyclophoridae (Wenz, op. cit., p. 470), Tornatellinidae, or Urocopidae (Pilsbry, op. cit., pp. 317-318), the presence of a diversified land snail fauna in the Paleozoic is highly significant.

Unfortunately there are practically no records of non-marine mollusks from the early Mesozoic and only a few from Cretaceous strata. It is not until the Paleocene and Eocene that extensive deposits of terrestrial and fresh-water gastropods are found. Many of the species recovered from these deposits unquestionably belong to modern genera and nearly all can be referred to existing families.

Modern families and many modern genera are represented in Cretaceous, Paleocene, and Eocene strata. Some faunal changes

have occurred on continents since then; for example, *Strobilops* was present in Europe from the Eocene to the Pliocene; the bulimulid(?) *Grangerella* in the Eocene of Canada and Wyoming; and Camaenidae (*Dentellocaraculus*) in the Eocene of Europe. All of them appear to have been replaced subsequently by more advanced taxa. In many other areas the present fauna is nearly the same as in the Eocene and Paleocene. Both the Bulimulidae and Strophocheilidae have been found in the Paleocene of Argentina (Parodiz, 1946, 1949); *Oreohelix* appears in the Cretaceous of Alberta (Pilsbry, 1939, p. 417); and *Polygyra* has been in America since the Cretaceous. There are many similar records scattered through the literature.

The only records of fossil land mollusks from large islands are from the Miocene of Santo Domingo (Pilsbry and Olsson, 1954) and Jamaica (C. T. Simpson, 1894; Morrison, 1955, p. 155). All of the shells are referable to *subgeneric* taxa living in the same areas today. The age of *some* of the Jamaican species is uncertain, but the Santo Domingo shells are undoubtedly fossils of Miocene age. From the limited evidence available, Pilsbry and Olsson (1954, p. 2) conclude that "... the Middle Miocene land shell fauna contained species closely like those of the Recent Fauna" and that "... Insular endemism was apparently about as marked in the Middle Miocene as in the Recent Faunas."

Study of the deep core drillings from Bikini and Eniwetok in the Marshalls and Funafuti in the Ellices revealed the presence of several species of endodontids (Ladd, 1957, 1958), all of which were referable to modern genera (*Beilania* and *Ptychodon*) and ranged in age from Lower Miocene to Pleistocene. The fossils were all recovered from drillings on atolls, yet the present-day endodontids are restricted to high islands and there are no authenticated records from low islands or atolls. Four of the species are referable to *Ptychodon* and this involves only a slight northward extension of its range (see fig. 26), while the fifth is a *Beilania* (see fig. 25), presently limited to the high Carolines, Palaus, Marianas, and Indonesia. The fossil species are only slightly differentiated from living species, but we do not know enough about the recent forms to evaluate their exact specific affinities.

These data suggest that in the Tertiary only minor evolutionary changes took place in the land Mollusca. Modern families were present in the Cretaceous and Paleocene; modern genera in the Eocene; modern subgenera in at least the Miocene; and modern species in the Pliocene. Evolutionary rates in the land Mollusca

from the Mesozoic on have been much slower than those in the vertebrates. The present families of land snails originated back in the Mesozoic or late Paleozoic and the adaptive radiation by which the land snails filled their ecological niches must have occurred at an even earlier date. Obvious exceptions such as the "explosive speciation" of the *Orthurethra* on the Hawaiian islands do not alter the basic evolutionary conservatism of the mollusks.

Such a conclusion is by no means original. It has been most brilliantly postulated by Pilsbry (1894, pp. xxxviii–xlvi) and subsequently confirmed by other malacologists. Since the first colonization of land by the plants, there have been several major radiations of land animals. The earliest would include the cryptozoic fauna of insects, other arthropods, and land snails which feed on decaying plant matter. Without a doubt their adaptive radiations greatly antedate those of the land vertebrates; that is, amphibians in the Carboniferous, reptiles in the late Paleozoic and early Mesozoic, birds in the Cretaceous, and mammals in the Tertiary.

The significance of this information was summarized by Van Dyke (1939, p. 256) in discussing the Coleoptera of North America: "Thus, the insects being of infinitely older stock than the higher vertebrates, we are justified in concluding that the history of their earlier migrations and distribution goes back very much further in geological time than does that of the mammals and birds. We can, in consequence, better utilize certain earlier geological and geographical changes than can the students of the higher vertebrates, who of necessity are limited to such changes as have taken place during the Tertiary." That similar conclusions apply to land snails has been recognized by Mayr (1940b, p. 197), Hesse, Allee and Schmidt (1951, p. 130) and several other vertebrate zoologists. Yet in discussing the origin and means of arrival of the fauna in the Greater Antilles, Darlington (1938) would consider the entire fauna "oceanic," since all the vertebrates can be accounted for by relying on overseas dispersal.

The Dispersal of Island-Dwelling Organisms

The spread of a species must be either through a continuous ecologically acceptable zone or by saltatory jumps over unfavorable environmental conditions. The movement of taxa through an ecological continuum is probably more of a theoretical ideal than a reality; nearly all extensions of distributional ranges involve the passing of some obstacle which has prevented spread in the past. The

varied nature of these "barriers to dispersal" and the means for circumventing them have been summarized by Hesse, Allee and Schmidt (1951, pp. 68-88 particularly). Few barriers are absolute for all organisms and the use of the term "filter zone" in reference to any given check on dispersal is perhaps more appropriate.

The ability of species to pass through filter zones, their "vagility," varies tremendously and what may be nearly impossible for one organism may present no problem for others. In general, passage must be by (1) their own locomotion or (2) passive dispersal by any one of several agencies. For land animals, perhaps the most effective filter zone is the open ocean, for many land dwellers are incapable of crossing open water by their own movement. Of the vertebrates, apparently the "primary freshwater fishes" are completely unable to pass salt water barriers (Myers, 1953b, p. 47) and amphibians cannot do so under their own power (Myers, 1953a; Inger, 1954, pp. 475-484). Many snakes, lizards, and crocodiles are strong swimmers; birds and bats can fly; and most mammals can swim short distances.

If there were no factor of passive dispersal, an "oceanic island" for vertebrates would have birds, bats, and a few reptiles, but no fresh-water fishes or amphibians, and probably no non-flying mammals. Obviously, passive dispersal has modified the fauna of many "oceanic islands" and there is a considerable literature devoted to the mechanisms which may be utilized for the passive dispersal of vertebrates. George Gaylord Simpson has discussed the passive dispersal of mammals and has given detailed analyses of the origin and dispersal of the present mammalian faunas. Discussion of the dispersal of vertebrates is not relevant to this study, since the New Hebridean vertebrate fauna is composed only of elements that are obviously introduced or are capable of crossing oceanic filter zones (see pp. 311-316).

Of the invertebrate phyla, spiders, insects, and land snails have been most frequently referred to in zoogeographic analyses. Spiders and land snails are, with few exceptions, strictly terrestrial animals and obviously cannot cross water barriers by their own locomotion. Most insects are winged organisms, although the ability for sustained flight is absent in many families. Despite limited powers of active dispersal, insects, spiders, and land snails are found on almost all islands, and in some areas have undergone extensive specific radiations. Most authorities explain their presence on "oceanic islands" as the result of passive dispersal by winds, ocean currents, or "accidental transport" on other organisms.

DISPERSAL OF SPIDERS

For many spiders the normal mode of dispersal is by wind. Young spiders spin strands of "gossamer" and are often carried through the air for a considerable distance by their "parachutes." Swarms of "ballooning" spiders are common and there are reports of spiders being captured in air "plankton nets" at heights up to 15,000 feet (see Zimmerman, 1948, p. 58). An important exception concerns the mygalomorph spiders, which do not utilize this means of dispersal. Gossamer-spinning spiders are found on nearly all Pacific islands, but mygalomorphs are recorded only from Melanesia and a single species is found in Samoa (Marples, 1953). Very primitive mygalomorphs live in New Zealand and New Caledonia.

DISPERSAL OF INSECTS

The passive dispersal of insects has been considered at great length by Zimmerman (1942; 1948, pp. 56-62). The taxa east of Fiji are all adapted for possible "accidental transport," but west of Fiji there are families, notably the scarab beetles and several Orthoptera, that seem to be ill-adapted for chance dispersal. Examples of a few Fijian and Samoan species whose habitat and habits seem to render overseas dispersal difficult are given by Chopard (1929) and Buxton (1930).

DISPERSAL OF NON-MARINE MOLLUSCA

The dispersal potentials of land and fresh-water mollusks have been summarized by Kew (1893). Very little data have been published subsequently, and most of the following account is condensed from Kew, with emphasis on the aspects misinterpreted by recent workers.

A fundamental distinction must be drawn between the chances for passive dispersal of (1) fresh-water and amphibious snails; (2) land snails; and (3) snails dwelling near the strand-line zone of beaches. Passive dispersal by other organisms is an important factor in colonization of fresh-water species, and storms probably are responsible for the mechanical spread of strand-dwellers, but the possibilities for passive dispersal of land snails seem to be infinitely less.

Fresh-water pulmonates.—For fresh-water snails of the families Physidae, Lymnaeidae, and Planorbidae, an important aid to colonization by the passive dispersal of individuals is the proven ability of self-fertilization. The impossibility of this for the fresh-water operculates may have an important effect on the relatively restricted ranges shown by the operculate taxa.

Within river basins undoubtedly the most important factor in the spread of a species is floods. Many examples of dispersal of fresh-water mollusks into flood-plain pools or even city streets have been recorded. The limitation of such transport is that it must always spread in a downstream direction and does not allow for interchange between river basins. The phenomenon of stream capture offers perhaps the best explanation of the faunal similarities between river systems, but of course it operates much less frequently than flood dispersal.

Of more direct importance to this study is the fauna of temporary woodland ponds, artificial pools, and fountains. The only mollusks normally found in these habitats are *Physa*, *Limnaea*, small planorbids, ancyliids, and sphaeriid clams (Boycott, 1936, p. 125). Species of these taxa are very widely distributed, and it is significant that they account for the vast majority of recorded instances of transport of mollusks by other organisms. Because of the reproductive habits of the Sphaeriidae (young retained in adult) the means for their passive dispersal into isolated waters are practically limited to transportation on other organisms. For the pulmonate families, the deposition of eggs on water plants allows the possibility of dispersal in both the egg and the adult stages. The presence of New Caledonian *Gyraulus* and *Physastra* (a *Physa*-like planorb) in the New Hebrides most probably is the result of passive dispersal by other organisms.

Fresh-water operculates.—Fresh-water operculates are usually absent from isolated bodies of water (Boycott, 1936, p. 126) and apparently are less apt to be carried by other organisms (Kew, 1893, pp. 85–86). The distribution patterns of the continental species are in rather close congruence with drainage systems. Euryvalent operculates such as the “*Neritina*” complex and the Thiariidae are capable of dispersal through the ocean, and many species have as wide a distribution as marine shells. The single New Hebridean fresh-water operculate, *Fluviopupa brevior* (Ancey), has relatives in the Fijis, on Lord Howe Island, and on Rapa. Its degree of toleration of salt water is unknown, but all Pacific localities are strictly fresh-water situations. The place of oviposition is unknown, but the reported habitat—still pools by the side of the Sarakata River—suggests the possibility of transport of ova or living adults in mud on the feet of aquatic birds. The evident insular endemism of *Fluviopupa* led Morrison (personal communication) to suggest generic separation of the Rapan shells, and it would indicate the relative infrequency of successful distribution by this method.

Fresh-water clams.—The methods of passive dispersal of the fresh-water mussels and its relative importance to them have long been a matter of controversy. In the species of continental areas, local movement of the larval glochidia by their fish host is undoubtedly the most important factor in dispersal. In explaining differences and similarities between stream systems, some would emphasize “stream capture” (see van der Schalie, 1939, 1945 for bibliography) while others suggest “accidental transport” by birds or mammals. The possibility of “bird transport” of unionids was considered at great length by Kew (1893, pp. 49, 57–61, 77–83) and McMichael (1958). In relation to the zoogeography of the Pacific, unionid distribution presents no usable evidence. The family affinities of the species are poorly understood, their reproductive habits are almost completely unknown, and locality records are few. No unionids are known from the Celebes, the Lesser Sunda Islands, or the Moluccas, but “unionaceans” reappear in Misool, New Guinea, the Solomon Islands, Australia, and New Zealand. The species from these areas are discussed later (see pp. 319–320).

Amphibious snails.—Before discussing the land snails, special mention must be made of *Succinea*. The famous case of the eggs of a snail found on the feet of a duck shot in the middle of the Sahara Desert (Kew, 1893, p. 157) has been widely cited. Indeed, Zimmerman (1942, p. 289; 1948, p. 60) submits this as proof that land snails are often carried by birds. The presence of living *Succinea* on birds has been reported (see p. 54, no. 1, this volume), but this is not surprising in view of the habitat of *Succinea*. The Succineidae live on the edges of marshes and in shallow swamps where aquatic birds congregate. In this habitat, the opportunities for passive dispersal on birds are even greater than those of most other fresh-water pulmonates. The supraspecific units of the Succineidae have extremely wide distribution and probably are the result of extensive “accidental transport” by other organisms.

Land snails.—The true land snails occupy a wide variety of habitats, and a survey of dispersal mechanisms by habitat types is perhaps most instructive. In regard to the Pacific islands, recognition of strand-line and shore vegetation types, arboreal species of the high island forests, and ground-litter forms of the forested areas cover the major divisions.

In all of the above categories the power of individual movement probably is of little importance in aiding distribution. The extreme localization of colonies in such snails as *Achatinella*, *Partula*, and

Cerion (Mayr and Rosen, 1956) emphasizes the effectiveness of even minor ecological barriers to movement by individuals. Boycott (1934, p. 6) commented on the restricted vagility of many English snails, although he mentioned others which seem to disperse rapidly. We know very little about the extent of individual movement by snails, but it probably is very ineffective in so far as crossing filter zones is concerned. The importance of this will be stressed again later in this paper.

SHORE-ZONE DWELLERS: With the actual dwellers in the beach litter above the high tide mark might also be classed the inhabitants of the low vegetation zone between the beach and the forested areas. During storms this area is often inundated by waves and the possibility for mechanical dispersal by currents is almost as great for these shore-dwellers as for the strand-line forms. The conclusions of Mayr and Rosen (1956) on the West Indian shore-dweller *Cerion* would apply equally well to certain Pacific Ocean taxa. Besides the truncatellids (no. 1, this volume, p. 197), ellobiids such as *Melampus*, the relatives of *Pleuropoma articulata* (Pfeiffer) (op. cit., p. 176), and *Omphalotropis setocincta* Ancey (op. cit., p. 200) probably will be shown to occupy similar stations and be exposed to mechanical dispersal. The "species" in these examples are all widely distributed and inhabit the areas nearest the shore. As in *Cerion*, probably they are extremely tolerant to immersion in sea water and are mechanically dispersed by storms comparatively frequently. Population of the Pacific Islands by these taxa is no problem, and their relatives which inhabit the forest zones of high islands could be secondary derivations from the widely distributed species. For most of the helicinids and assimineids of the Pacific Ocean fauna it is conceivable to recognize such an origin. Operculates seem best able to withstand immersion in sea water (Kew, 1893, p. 121) and mechanical dispersal by storms and ocean currents provides the most plausible explanation for widely distributed taxa.

FOREST SNAILS: The situation is entirely different in regard to forest snails. Of the European forest snails tested by exposure to salt water (Kew, 1893, pp. 120-121) extensive toleration of immersion could be demonstrated only for *Helix pomatia*, which had secreted a heavy epiphragm. Species which live in partially arid areas and secrete heavy epiphragms could conceivably withstand several days in sea water and survive being cast up on the shore of an island. In continental areas, rivers in flood often transport shells for a considerable distance (Kew, 1893, pp. 138-145), although probably with

a higher mortality rate than among fresh-water species. I have observed two cases of changes in local distribution which seem to be most plausibly explained by flood dispersal. The logical extension of a belief in the spread of land animals by floods is the concept of natural rafts of large trees and masses of vegetation populating oceanic islands with terrestrial life. This theory was postulated for vertebrates by Matthew, and its possible importance for snails has been discussed by Kew (1893, pp. 120-138). In the Pacific region, ocean currents are against movement from New Guinea to the islands, but rather favor dispersal *from* Polynesia *toward* New Guinea. More important would be the problem of crossing the beach and low elevation zones, even granting survival of a long ocean voyage. Whereas a rafted reptile could "stagger" to the safety of the forest, it would be impossible for a forest snail to cross even a few feet of mangrove or beach zones (Pilsbry, 1921). In areas such as southern Florida, the presence of *Liguus* (a large arboreal bulimulid which aestivates by cementing itself to a tree limb) is undoubtedly the result of "rafting" from Cuba (Pilsbry, 1946b, p. 46). A parallel with the arboreal *Placostylus* at once suggests itself, but the aestivation habits of *Placostylus* are unknown, and the evolutionary sequence in *Placostylus* is a strong argument against any such mode of dispersal.

For snails of the forest floor, rafting is unacceptable as a theory of an effective means of dispersal. The strand-line dwellers are adapted for retention of moisture and prevention of desiccation; conversely, these same mechanisms would serve to exclude salt water. The snails of the humid forest floor are restricted to this area because of their inability to retard loss of moisture effectively. They would be unable to avoid direct contact with salt water during an ocean "voyage." Their eggs are laid in the soil, or, in the case of the carinate Endodontinae, *within the umbilicus of the adult shell*. Nobody who has seen snail eggs could possibly conceive of their surviving any contact with salt water, much less an ocean-crossing on a natural raft.

The same difficulties in postulating "natural rafts" apply to such arboreal snails as *Partula* and the tornatellinids (excepting the widely distributed terrestrial forms). The ovoviviparous *Partula* and *Achatinella* (a derivation from the tornatellinids) are limited to very humid areas and almost certainly show little or no resistance to immersion in sea water. Arboreal snails have been developed only in tropical areas with great humidity. Although such Neotropical taxa as *Orthalicus* and *Liguus* cement themselves to tree limbs during the dry season and are thus "often" rafted on trees, their *unreflected aperture seems to be an adaptation aiding such attachment*. The

strongly reflected lips in *Placostylus* and *Partula* probably indicate that these taxa do not cement themselves to tree limbs and thus cannot be considered as being adapted for raft dispersal.

The spread of the Pacific Ocean arboreal species by winds may be more important. Kew (1893, pp. 145-154) considered the possibility of dispersal of land mollusks by hurricanes and concluded that such transport is possible for "particularly those living among vegetable debris, dead leaves, and the like." (Kew, 1893, p. 154.) This form of transport (either by subsequent ocean currents or wind dispersal) would be particularly effective for the strand-dwellers, the forms in the drier low areas of the islands, and the strictly arboreal taxa. *Partula* rests clinging to the under sides of leaves, and this habit provides excellent possibilities for dispersal by winds, contrary to the belief of Crampton (1916). For species inhabiting the moist litter and soil of the high forest zones, the possibilities of dispersal by hurricanes are much less. The slight protection of the tree cover and the relatively great cohesion of the moist soil would greatly lower the chances for wind dispersal (see also Jacot, 1934, pp. 85-92). Forms found fastened to *dry leaves and loose ground cover* would have the best opportunities for wind dispersal.

Probably the least important agency for effecting dispersal of land snails is passive transport by other organisms. The recent activities of man form a singular, but immediately recognizable, exception. The fauna of low coral atolls such as Makatea (C. M. Cooke, 1934) probably owes much to the Polynesian voyagers, just as the "tropical tramps" (see p. 209, no. 1, this volume) represent Caucasian influence in the Pacific. The species distributed by man are easily recognizable as such and have been omitted from the zoogeographic discussion for that reason. With the exception of *Succinea*, records for passive transport of land snails are almost non-existent. The operculate land snails could conceivably catch a bird's toe or insect's foot between the operculum and shell lip and thus be transported. Indeed, the European *Pomatias elegans* has been found attached to a bumblebee (Boycott, 1934, p. 6). For the non-operculates, fewer opportunities are afforded. Kew (1893, pp. 154-165) suggested that live snails (or eggs) might survive in birds' crops and be accidentally liberated upon the death of the bird in another area. Bondeson and Kaiser (1949, pp. 268-270) could not confirm this with domestic ducks, but they showed that fresh-water operculates can pass through fish unharmed. Most birds crush the shell or extract the animal before feeding on snails, and the non-operculates, even if swallowed alive, would have little chance of avoiding the digestive juices.

An apparent exception to the possibility that snails "hitch rides" on birds concerns the sub-Arctic genus *Vitrina* and the conchologically similar *Helicarion*. *Vitrina* has been reported on birds at least twice (see Boycott, 1934, p. 6, and Arch. Moll., 80: 85). *Vitrina* forms one of the few Nearctic elements in the Hawaiian fauna (see H. B. Baker, 1941, pp. 349-352) and is probably derived from transport by a bird such as the golden plover. Similarly, a species of *Helicarion* has been seen on the wingcase of a beetle in Queensland (Kew, 1893, p. 155). It is thus very significant that *Helicarion* represents the only "modern" element in the faunas of southwest Australia and Tasmania.

LAND SLUGS: In comparison with snails, slugs have even fewer possibilities for dispersal. The lack of a protective shell would make overseas transport by currents or rafts impossible. Although introduced Holarctic species have flourished on Pacific islands, Australia, and New Zealand, it is significant that the only native slugs in the Pacific area are the relict family Athoracophoridae of Melanesia and New Zealand and the Rathouisiidae of Indonesia, New Guinea, and Queensland. No slugs are native to any of the "oceanic" islands.

Summary.—The wide distribution of fresh-water pulmonates, sphaeriid clams, *Succinea*, euryvalent fresh-water operculates, shore vegetation species, and, to a lesser extent, stenovalent fresh-water operculates, is caused by an ability to utilize means of passive dispersal. The greater endemism of forest snails, particularly those of the humus zone, reflects a comparative inability to use such means.

LAND SNAIL FAUNAS OF THE PACIFIC OCEAN AREA

Distribution maps of the zoogeographically important genera and families of Pacific land snails are presented in figures 12-28. The maps are based on data from specimens in Chicago Natural History Museum and the University of Michigan Museum of Zoology and on records from the literature. The scale of the maps and paucity of locality data prevent the delineation of boundaries on the large islands of Borneo, Celebes, Java, New Guinea, and Sumatra. For the same reasons, distributional limits in Australia are only approximate. Utilizing the raw data in these maps and the many faunistic surveys in the literature, I have attempted to interpret the gradual shifts in families and genera which have taken place between the mainland of southeast Asia and the Marquesas, and to present summaries of the land snail faunas of certain critical areas as they compare with the New Hebridean fauna.

A great handicap to the survey is the fact that the minute snails of the Pacific islands have been comparatively well studied, but the similar fauna of Indonesia is so little known that it is impossible to correlate generic units and thus determine the degree of relationship which exists.

General Survey

For all groups of organisms the Malay Archipelago represents the start of the great tropical region extending eastward through Polynesia. The path of dispersal has been from Malaya to New Guinea. Then the emigrants split into several branches which moved into Australia or out to the Pacific Islands with a gradual attenuation of the Malayan elements. The nature and path of this expansion were recognized as long ago as 1825 by the botanist Lesson (see Hedley, 1899, pp. 397, 398). New Zealand, Australia, and, to a lesser degree, New Guinea, have endemic organisms which are unrelated to present-day Malayan taxa. The delineation of the boundary between the areas marked by the dominance of the Malayan and Australian biotas has been one of the major interests of biogeographers (see Scrivenor, et al., 1943, and Mayr, 1944, for references). The change from the Oriental to the Australian bird and mammal faunas lies between "Wallace's Line" and "Weber's Line." Botanists, however, would include New Guinea in the Malayan region, rather than in the Australian (for example, Good, 1953).

Distribution patterns of genera and species of land snails within the Indonesian and Papuan areas are exceedingly complex, and interpretation of this material is well beyond the scope of this paper. Certain facets of family distribution, however, are in striking accordance with botanical features.

SOUTHEAST ASIA TO NEW GUINEA

On the mainland of southeast Asia there is an admixture of Indian and Chinese taxa with what can be termed the start of the Malayan fauna (A. H. Cooke, 1895, pp. 300, 305, 306). The larger helicarionid snails (fig. 15), rathouisiid slugs (fig. 17), cyclophorid operculates, carnivorous streptaxids, many unique pupillids, camaenids, and the mesurethran relict Corillidae dominate a rich fauna. In the area between Burma and the end of the Malay peninsula the Corillidae (fig. 12), the Streptaxidae (fig. 12), and many cyclophorids reach their southern limits. No streptaxids or corillids are found on Java (van Benthem Jutting, 1948, 1950, 1952, 1953a, 1956) or Sumatra.

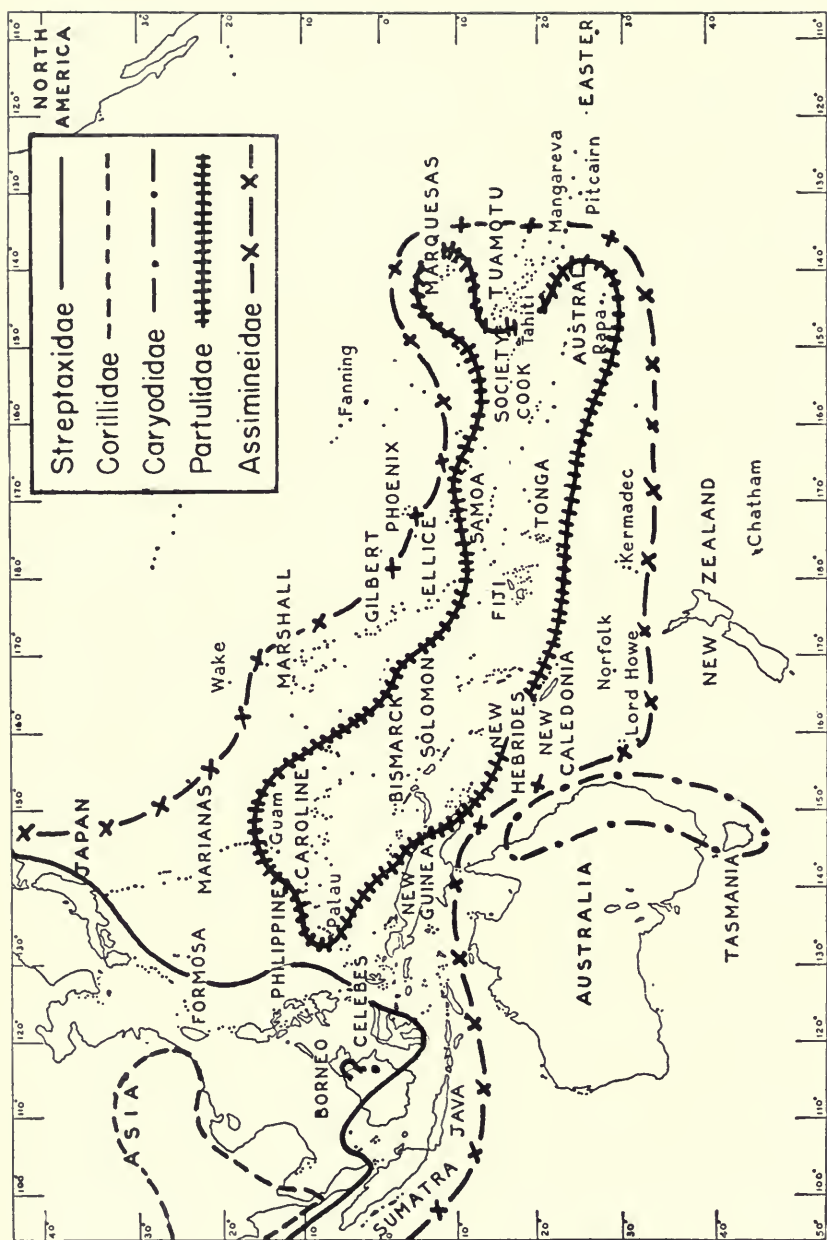


FIG. 12. Range of Streptaxidae, Corillidae, Caryodidae, Partulidae, and Assimineidae.

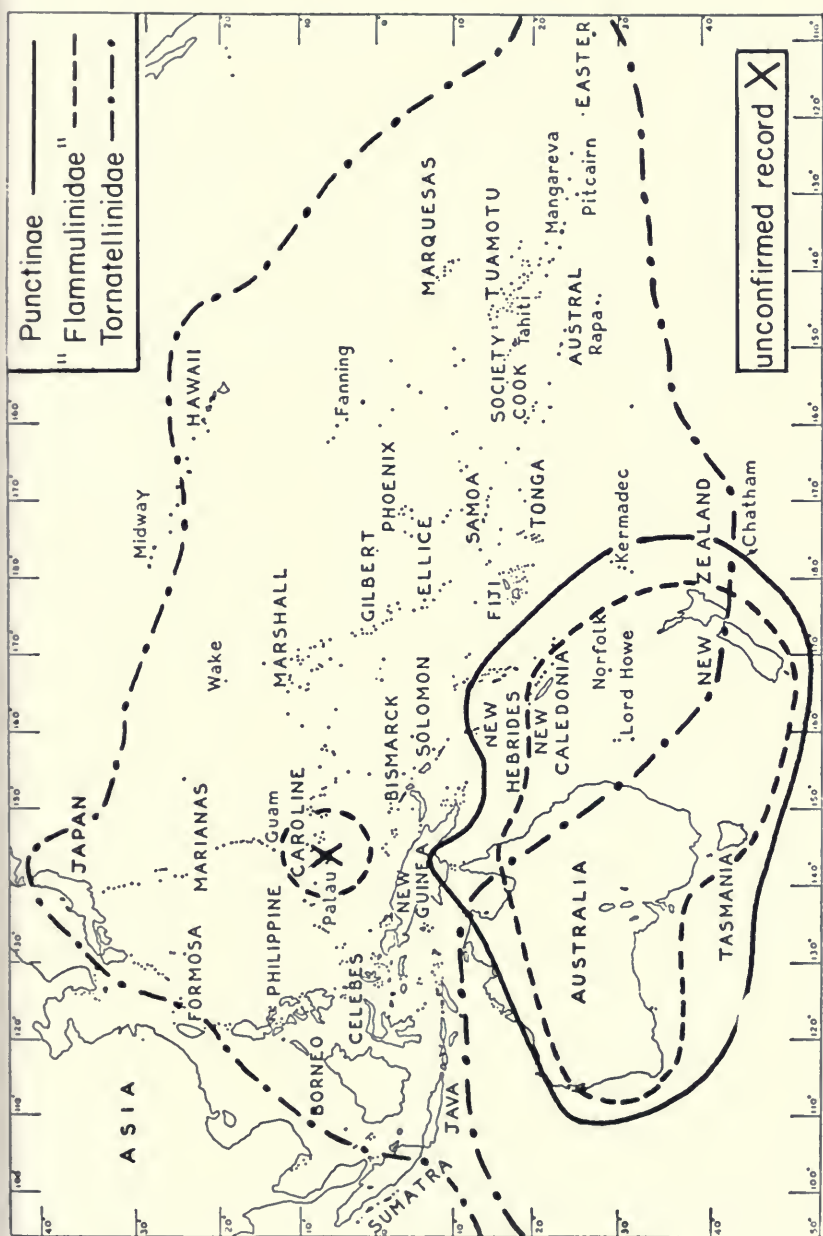


FIG. 13. Range of Punctinae, "Flammulinidae," and Tornatellinidae.

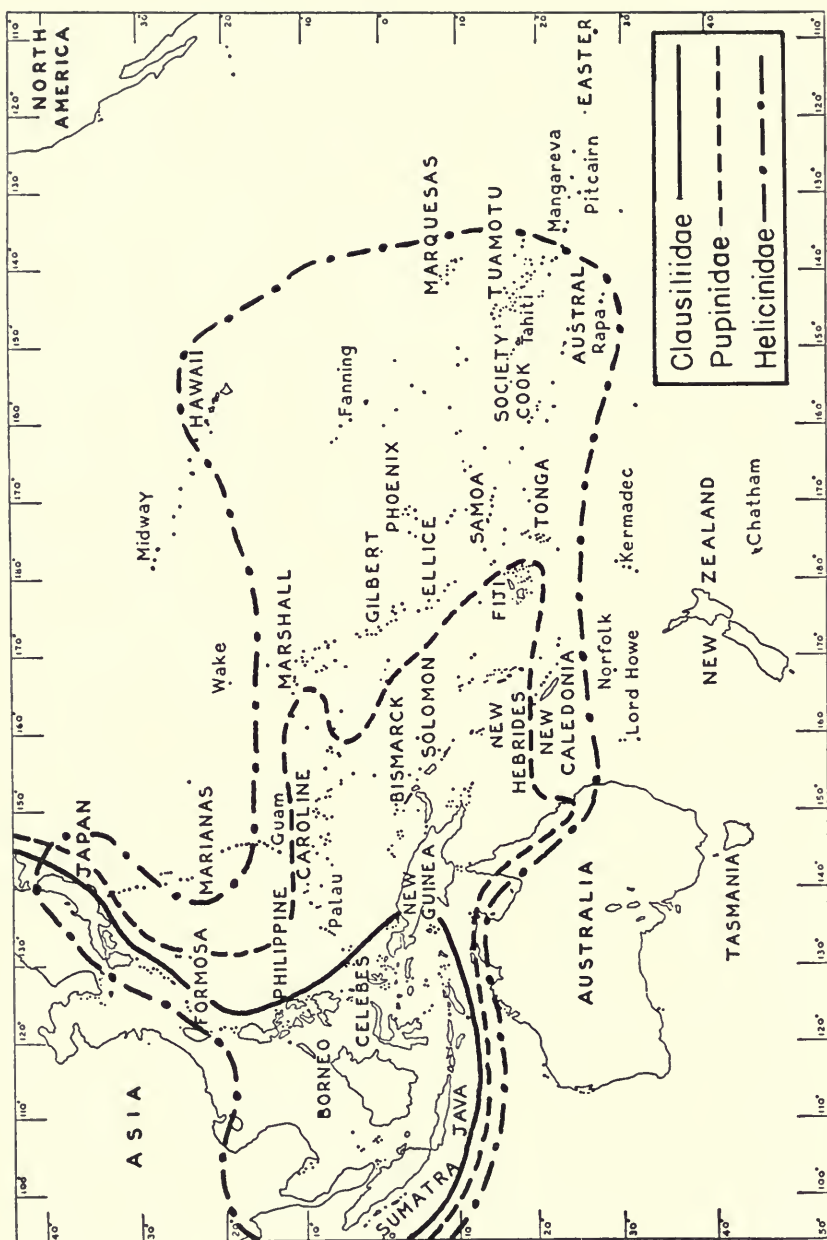


FIG. 14. Range of Clausiliidae, Pupinidae, and Helicinidae.

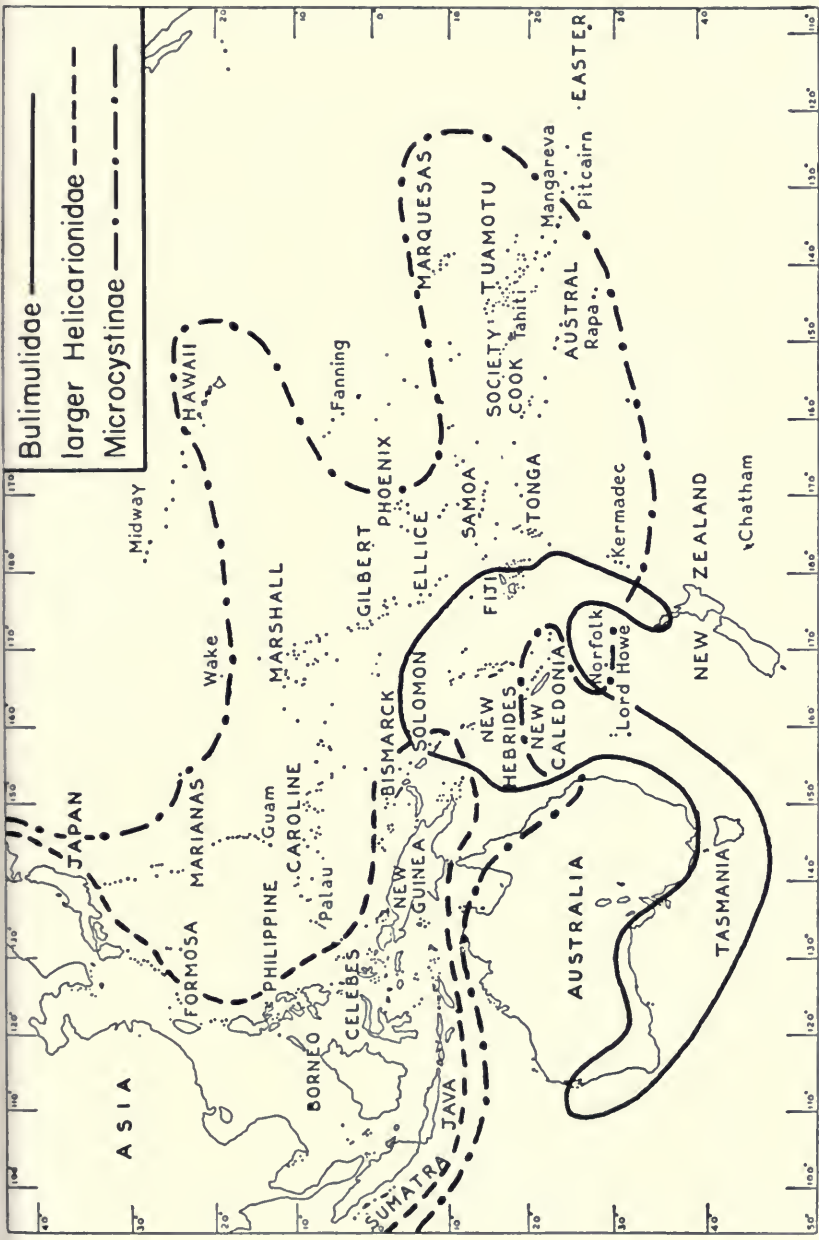


FIG. 15. Range of Bulimulidae, large Helicarionidae, and Microcystinae.

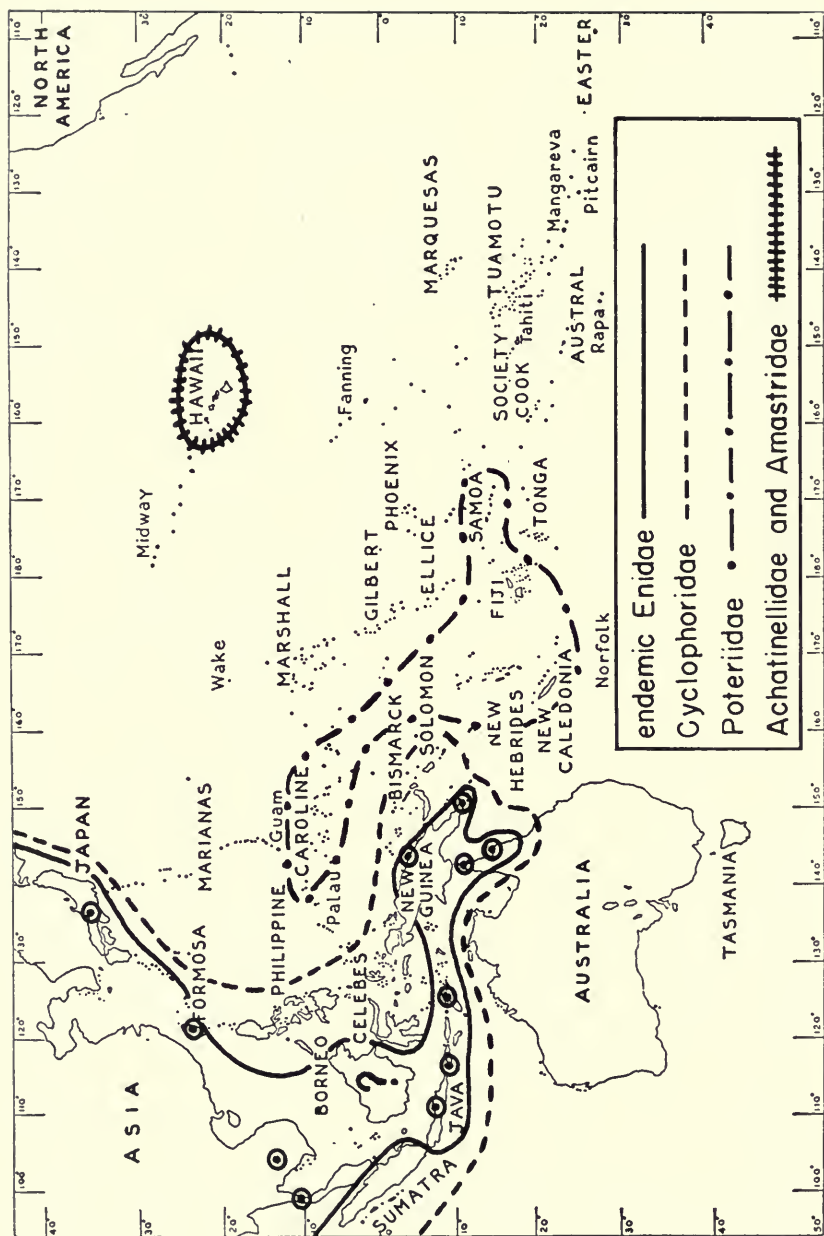


FIG. 16. Range of endemic Enidae, Cyclophoridae, Poteriidae, Achatinellidae, and Amastridae.

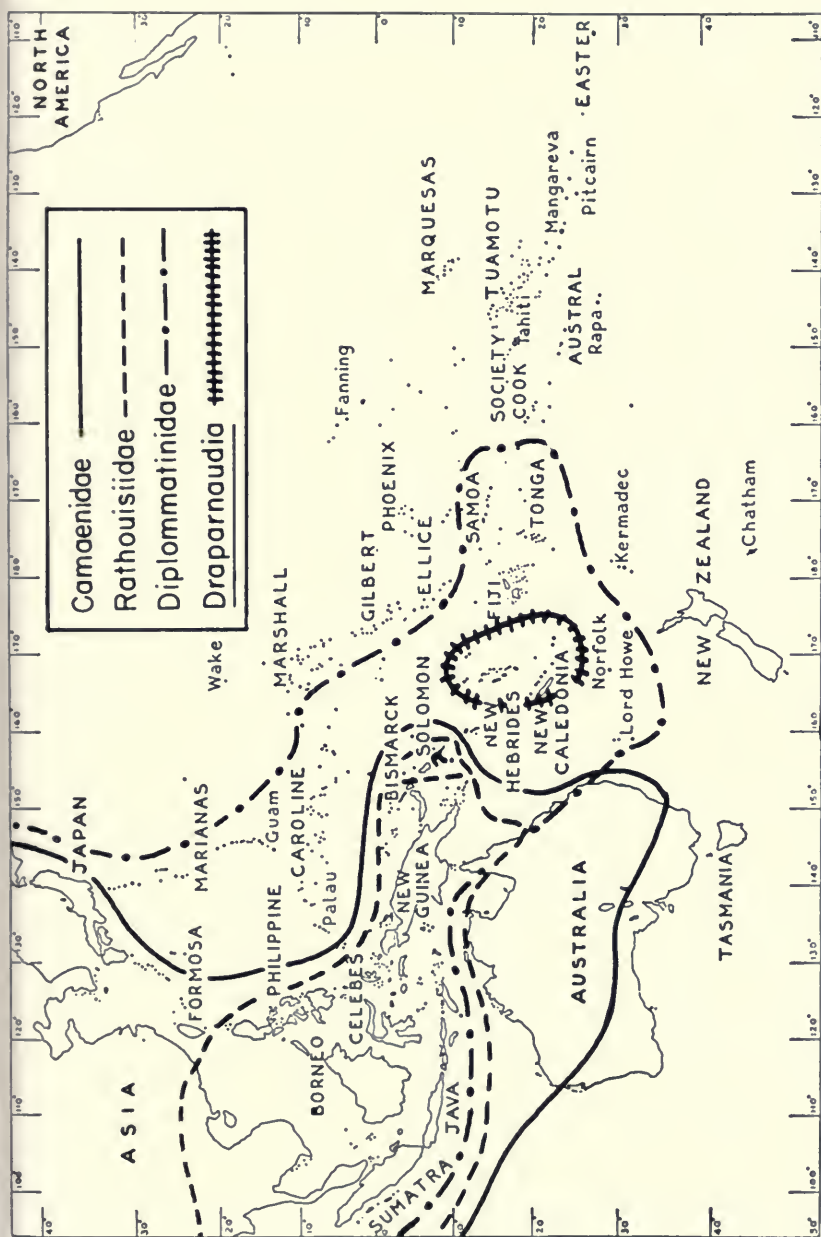


FIG. 17. Range of Camaenidae, Rathouisiidae, Diplommatinidae, and *Draparnaudia*.

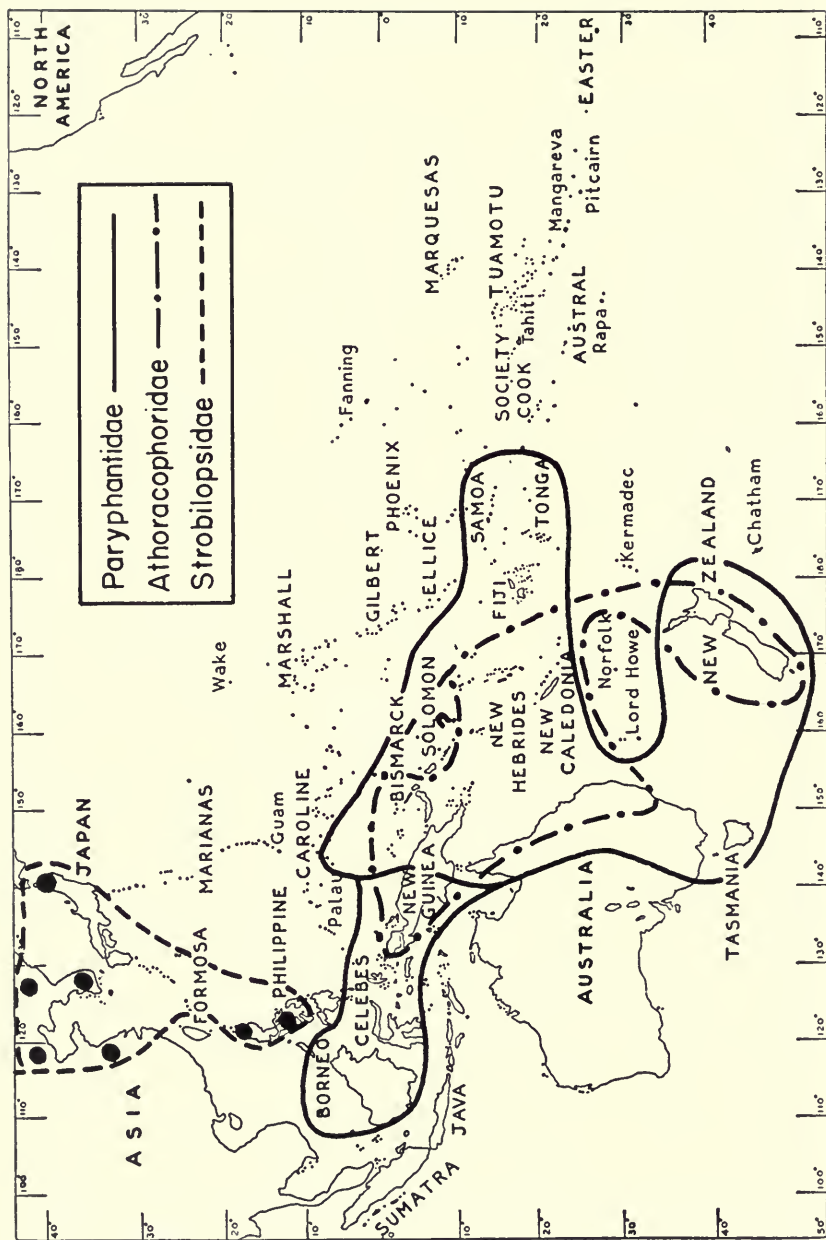


Fig. 18. Range of Paryphantidae, Athoracophoridae, and Strobilopsidae.

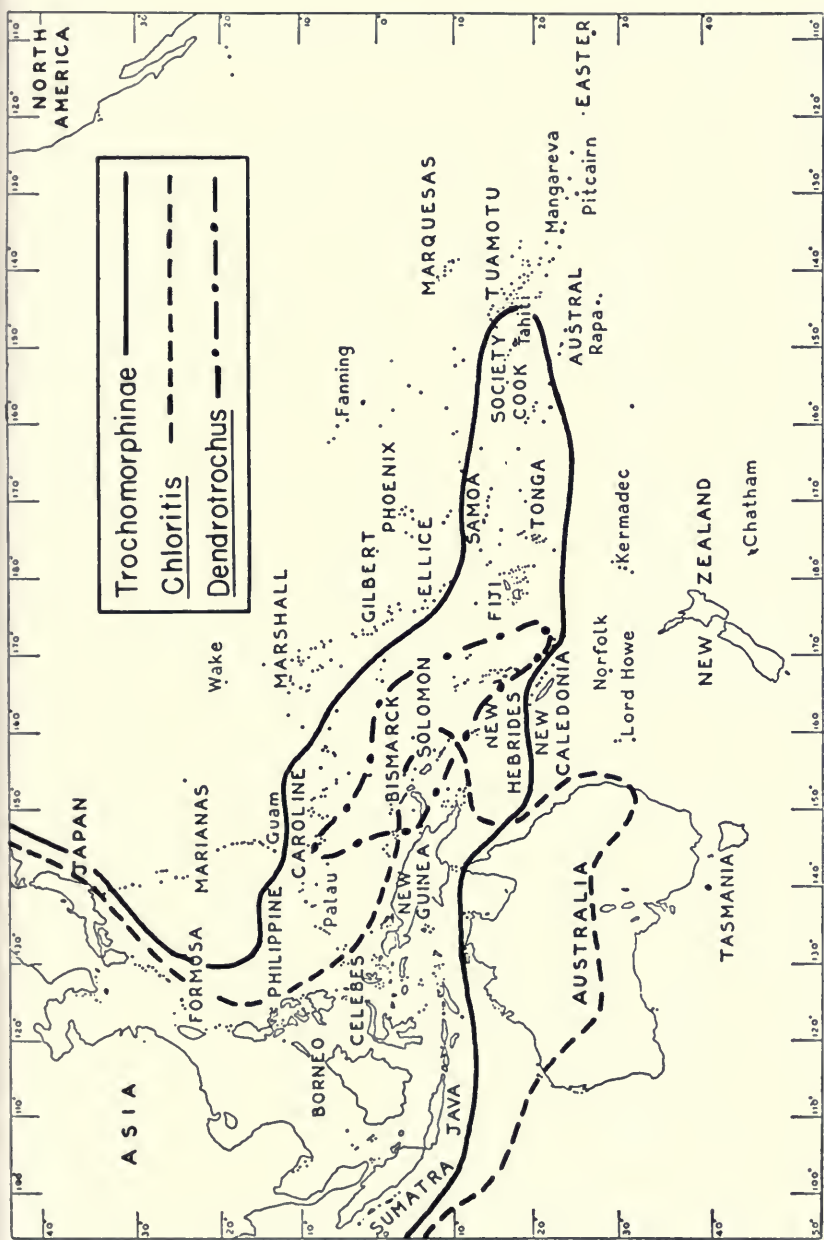


FIG. 19. Range of Trochomorphae, *Chloritis*, and *Dendrotrachus*.

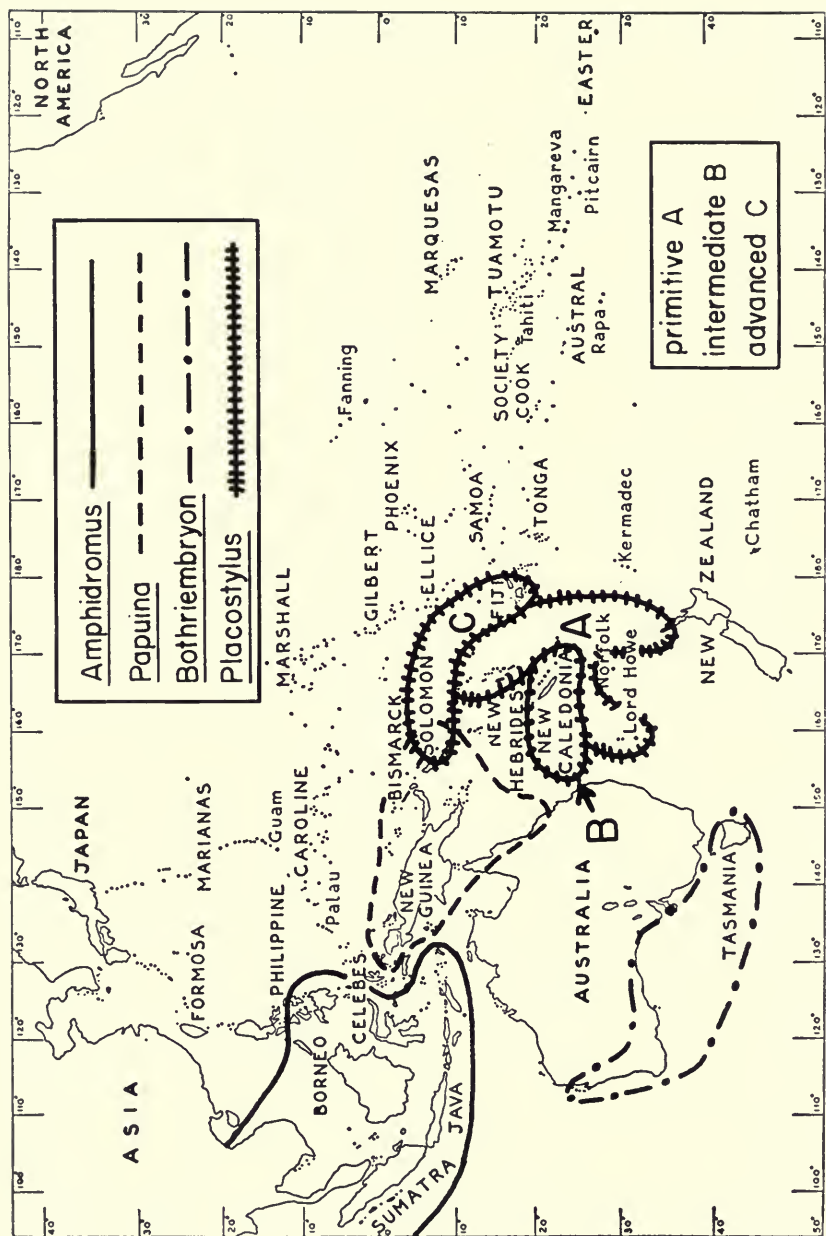


FIG. 20. Range of *Amphidromus*, *Papua*, *Bothriembryon*, and *Placostylus*.

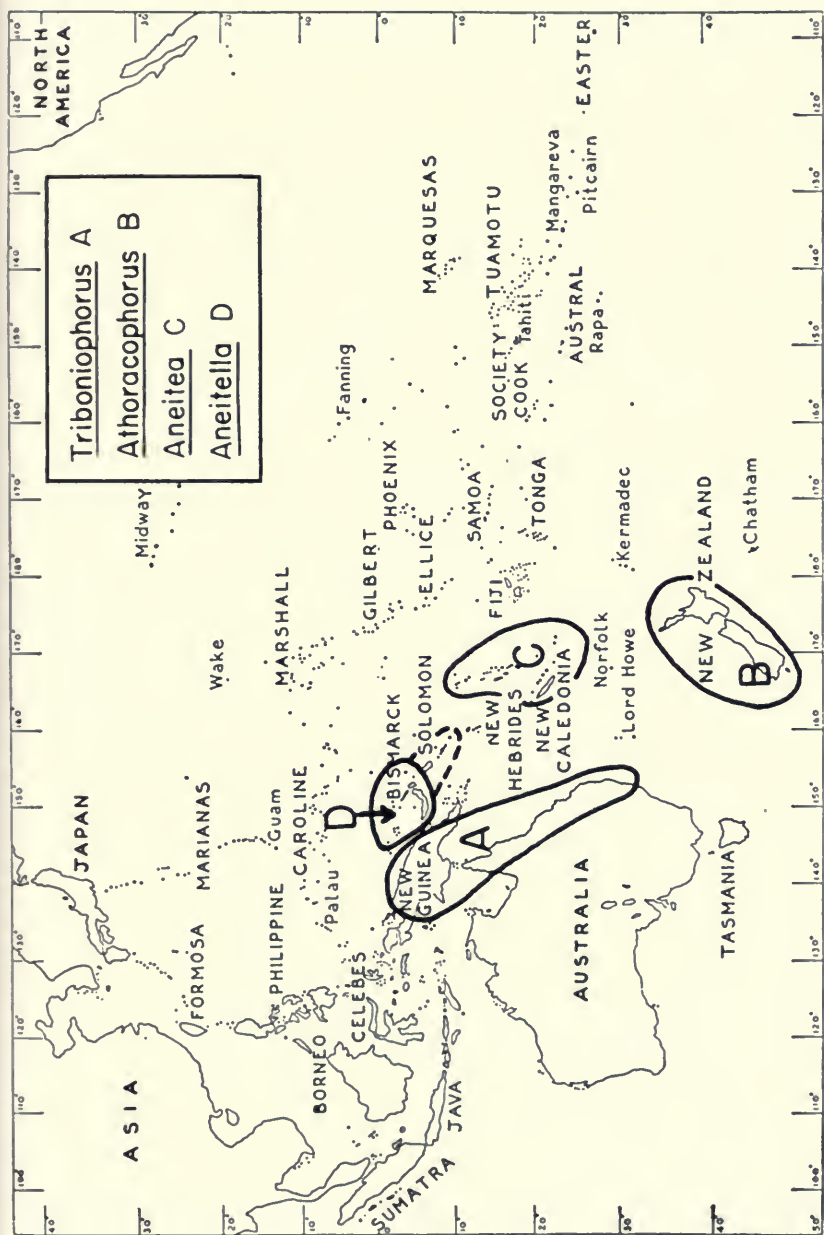


FIG. 21. Range of genera of Athoracophoridae.

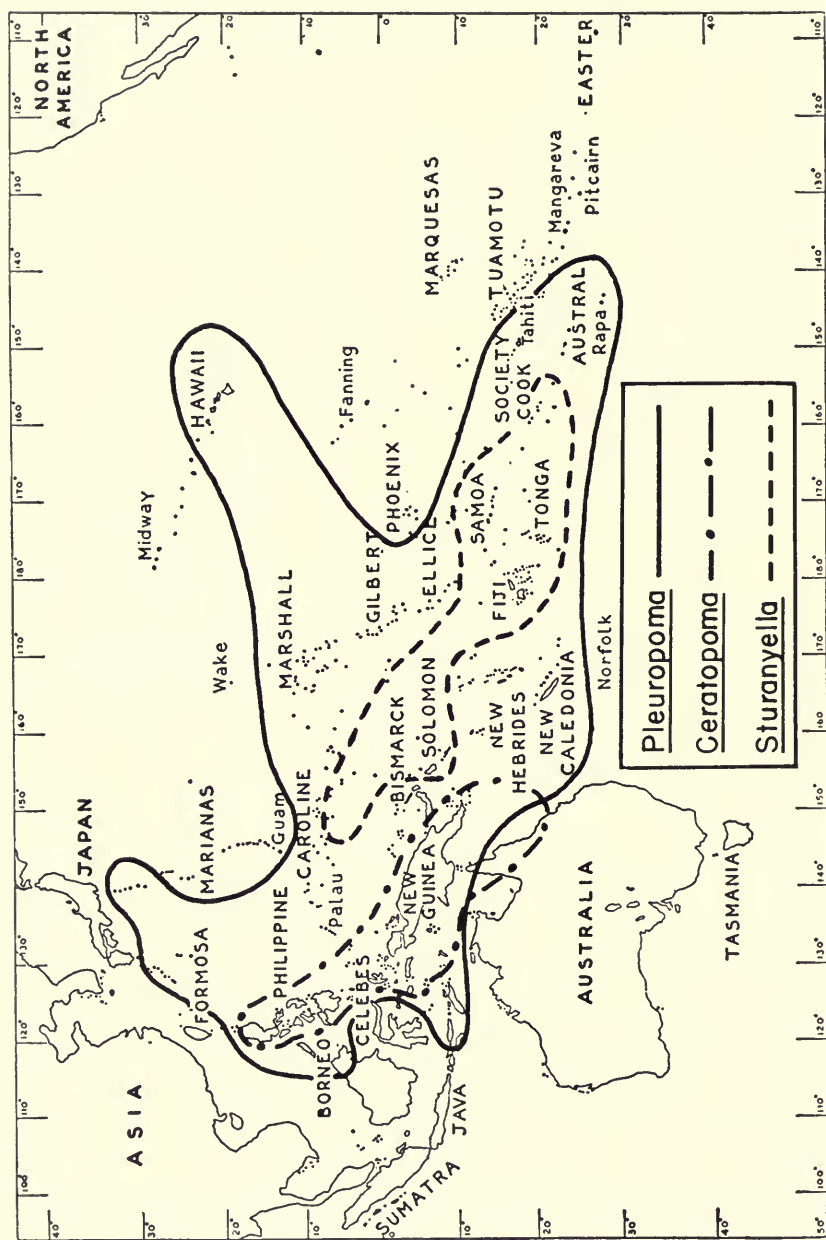


FIG. 22. Range of *Pleuropoma*, *Geratopoma*, and *Sturanyella*.

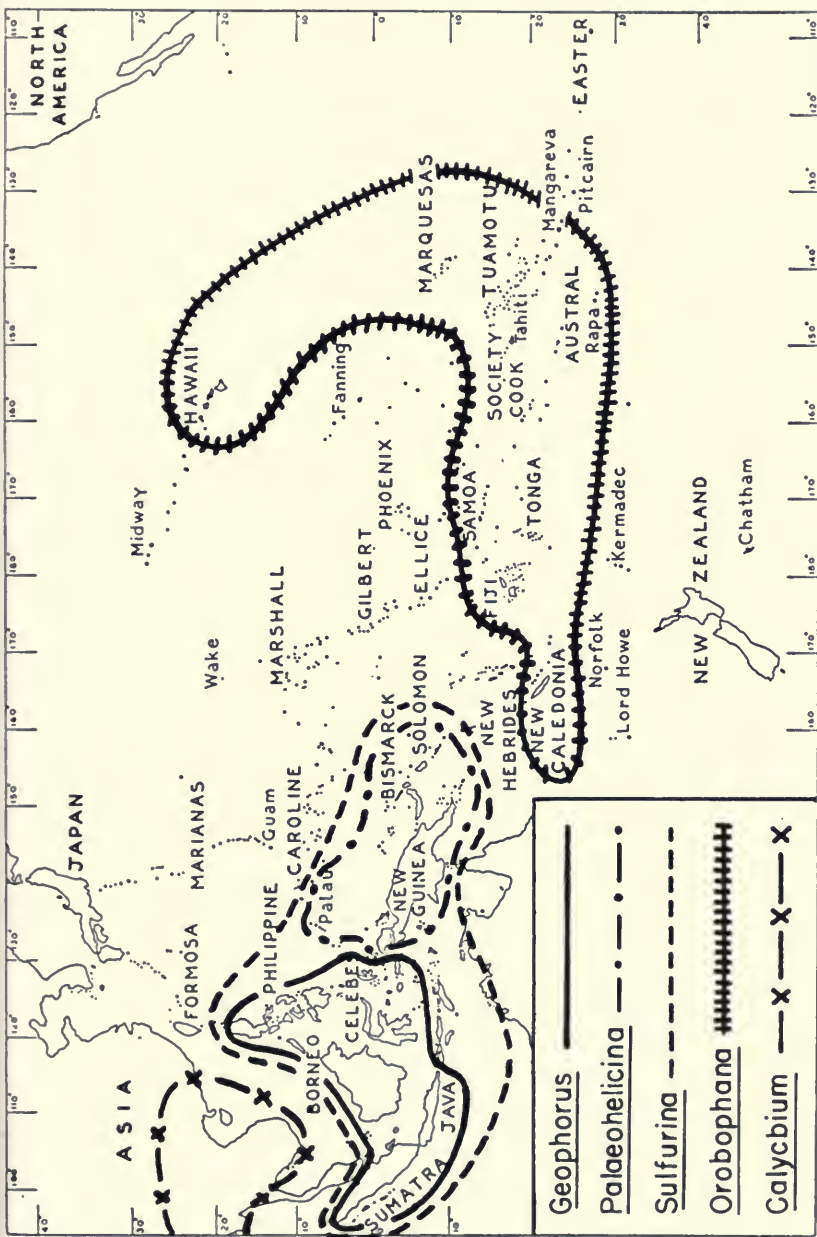


Fig. 23. Range of *Geophorus*, *Palaeohelicina*, *Sulfurina*, *Orobophana*, and *Calycbium*.

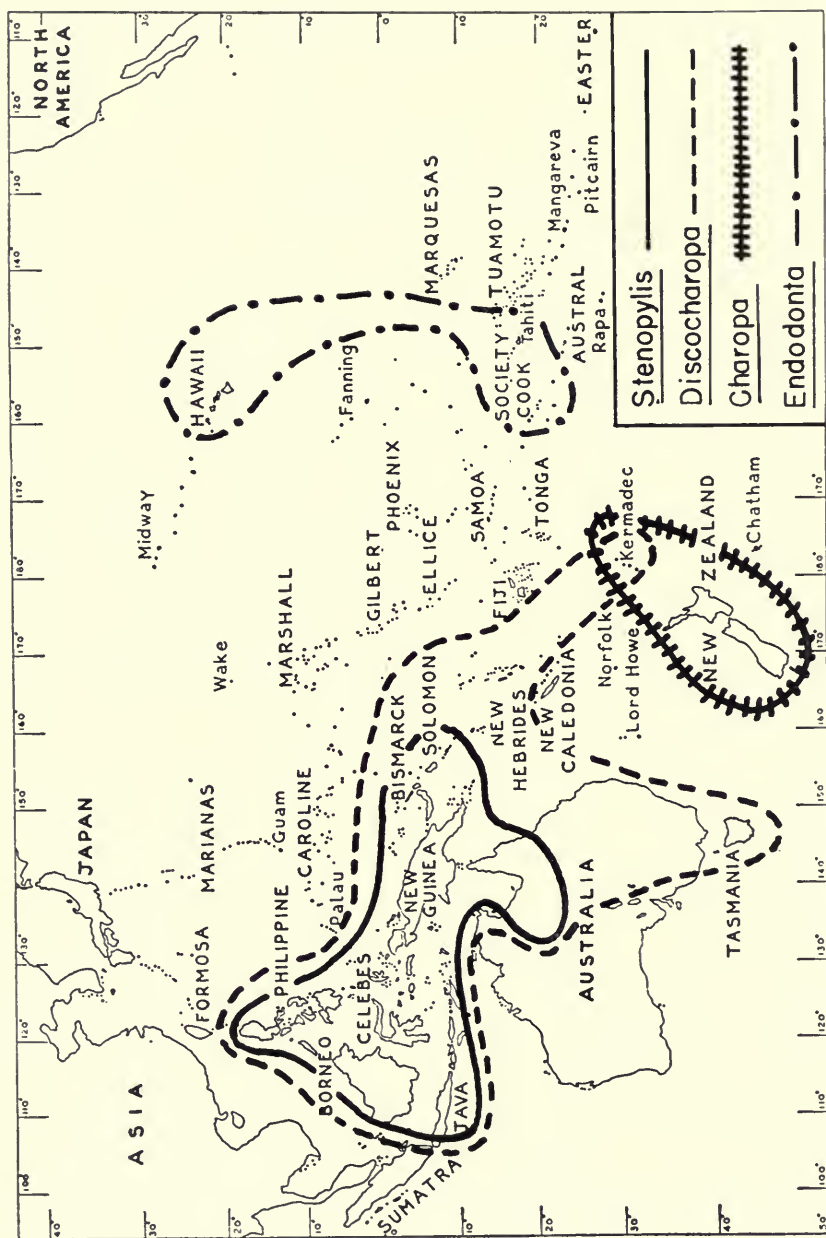


FIG. 24. Range of *Stenopylis*, *Discocharopa*, *Charopa*, and *Endodonta*.

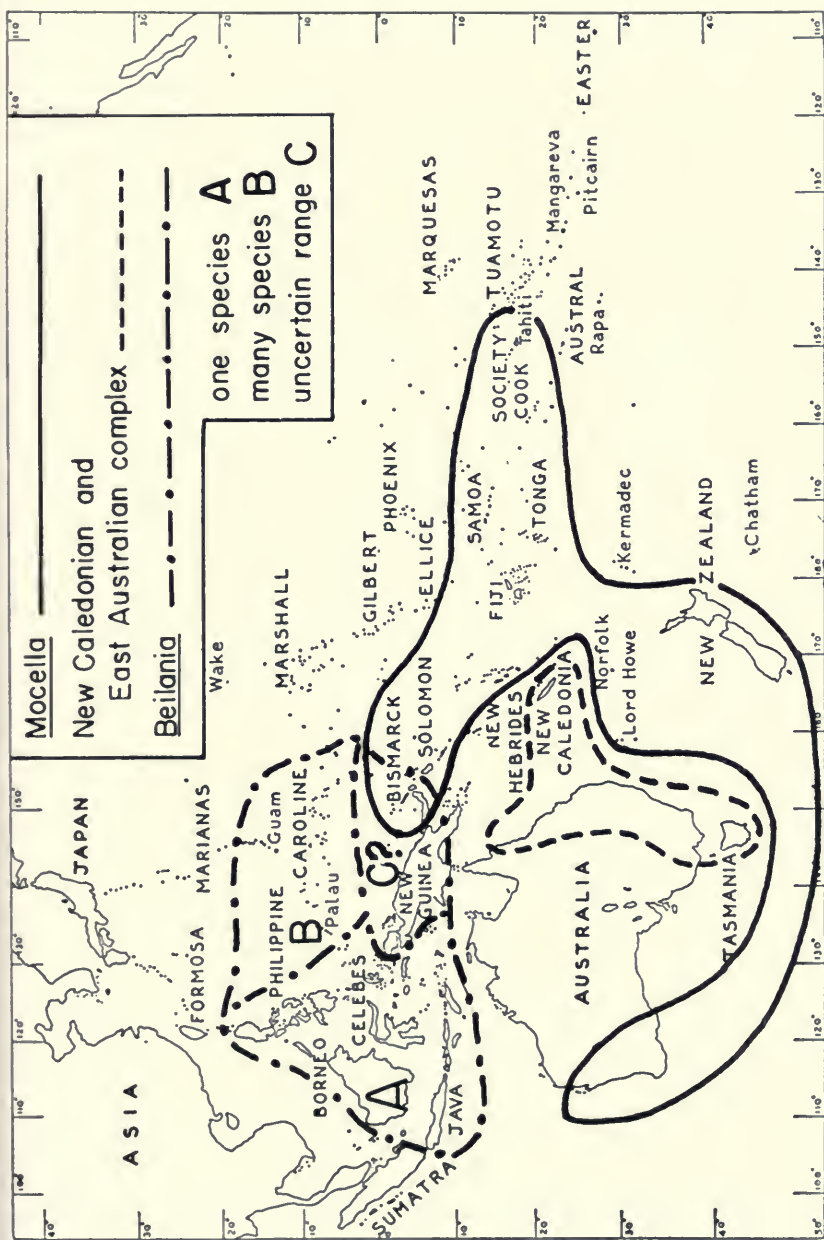


FIG. 25. Range of *Mocella*, New Caledonian and East Australian complex, and *Beilania*.

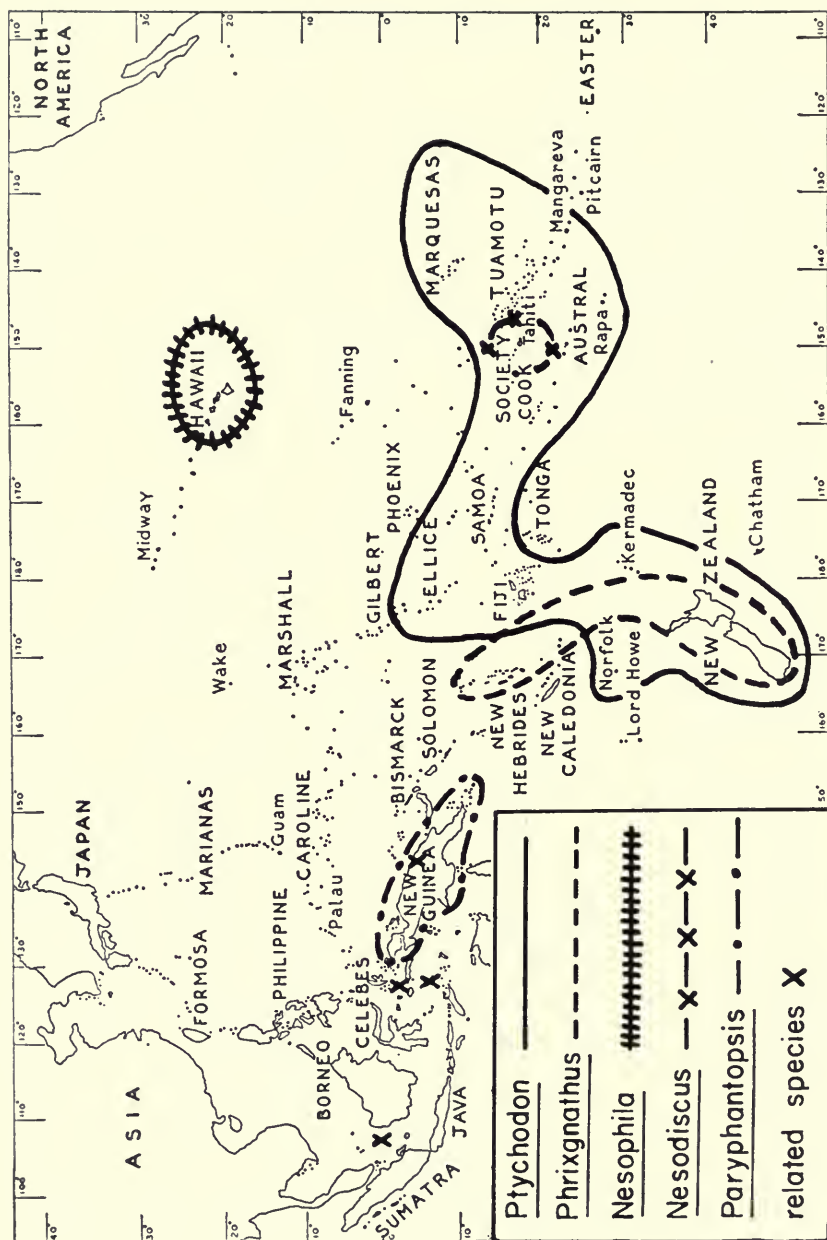


FIG. 26. Range of *Ptychodon*, *Phrixgnathus*, *Nesophila*, *Nesodiscus*, and *Paryphantopsis*.

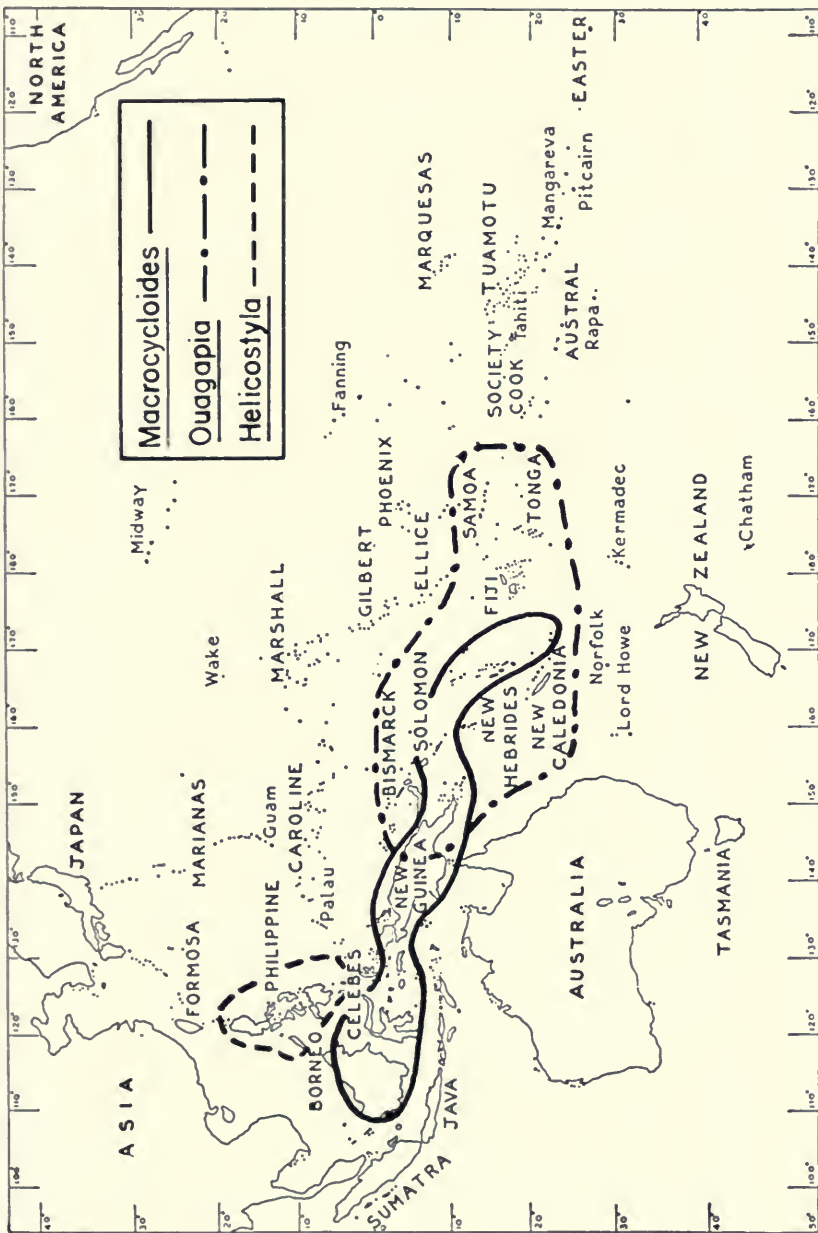


FIG. 27. Range of *Macrocyclus*, *Ouagapia*, and *Helicostyla*.

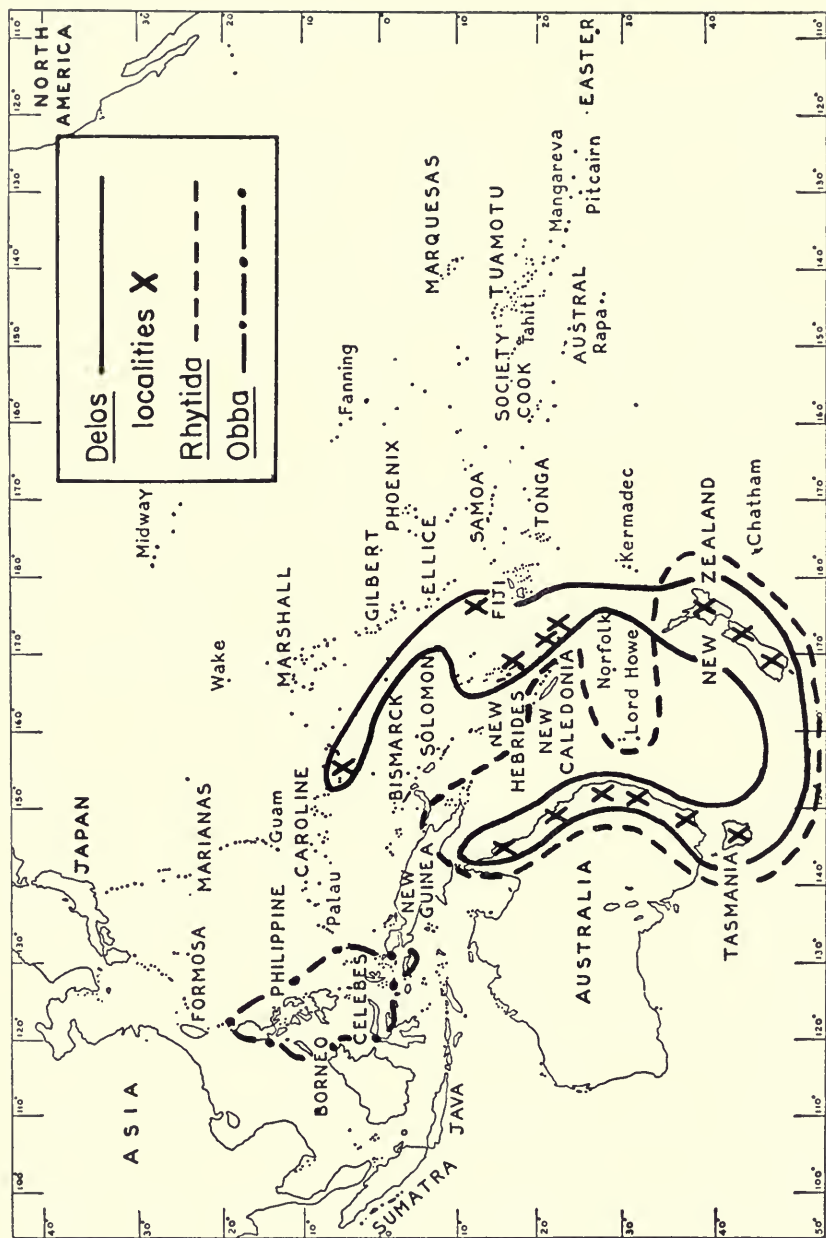


FIG. 28. Range of *Delos*, *Rhytida*, and *Obba*.

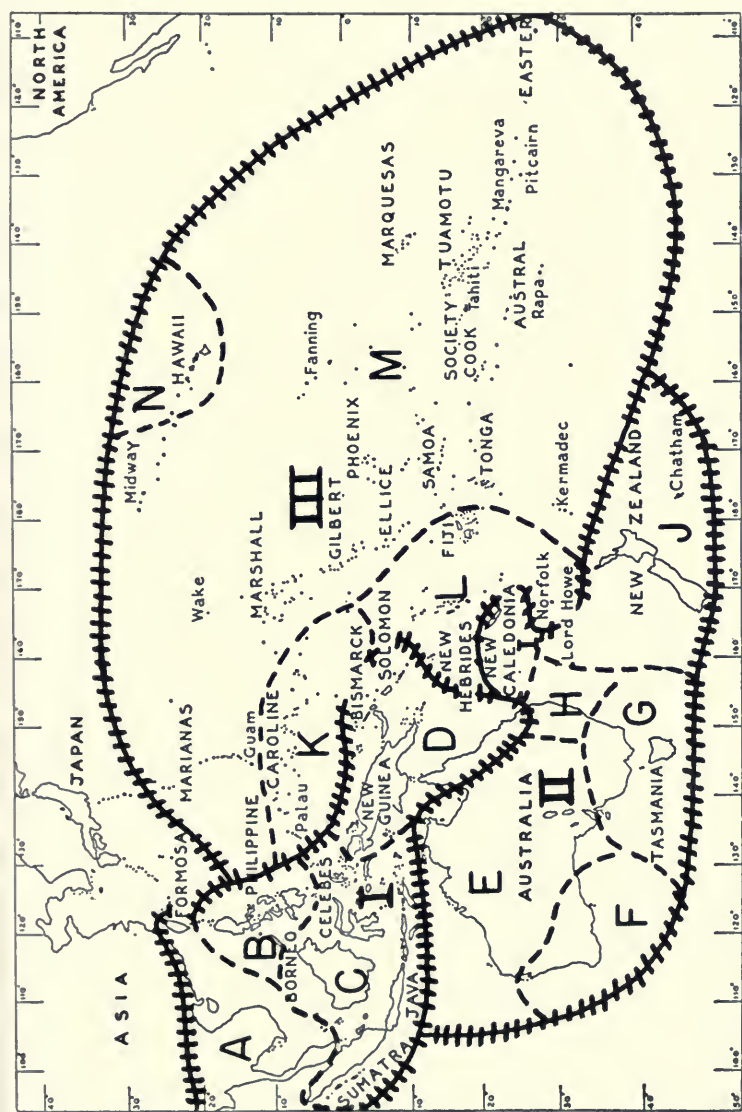


FIG. 29. Land snail regions of the Pacific Ocean.

I. PALAEO-ORIENTAL: A, Indo-Chinese; B, Philippine; C, Indonesian; D, Papuan. II. SOUTHERN RELICT: E-H (see Iredale 1937a); I, New Caledonia; J, New Zealand. III. PACIFIC ISLAND: Transition Zone: K, Micronesian; L, Melanesian. Oceanian Zone: M, Oceania; N, Hawaii.

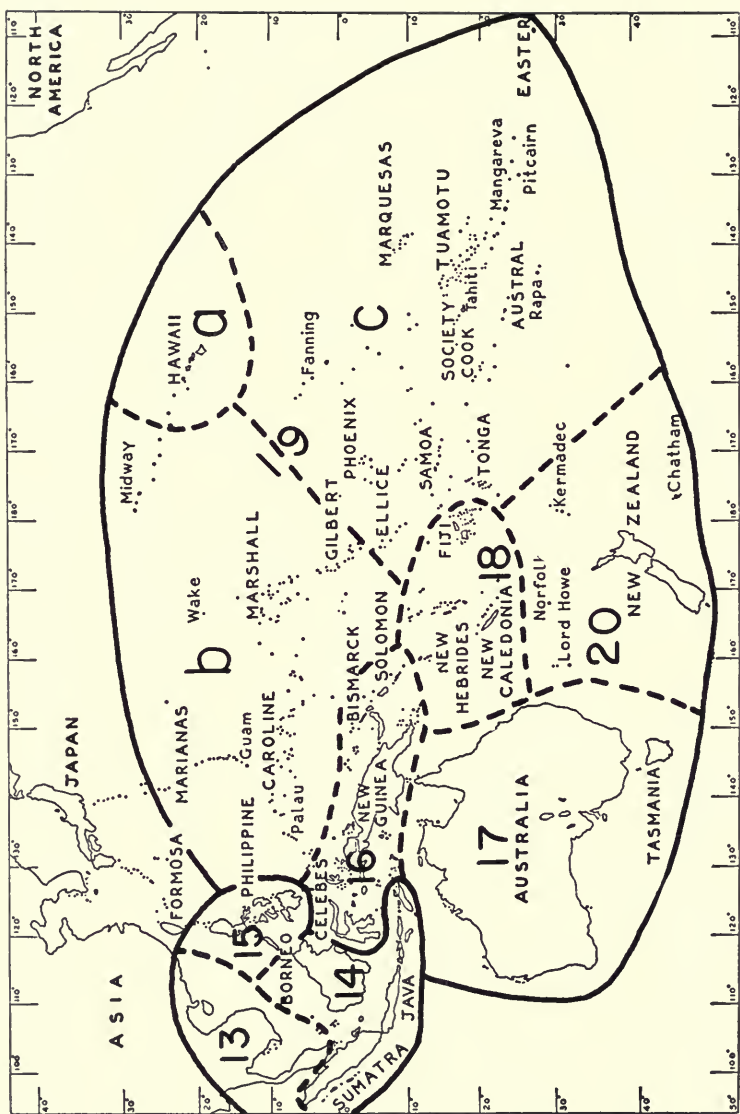


FIG. 30. Land snail regions of the Pacific Ocean (after P. H. Fischer, 1880-87).

PALÉOTROPICALE ORIENTALE: 13, Indo-chinoise; 14, Indo-malaise; 15, Philippinienne. AUSTRALIENNE: 16, Austro-malaise; 17, Australienne; 18, Austro-Polynésienne; 19, Polynésienne (*a*, Hawaï; *b*, Micronésie; *c*, Polynésie); 20, Néo-Zélandaise.

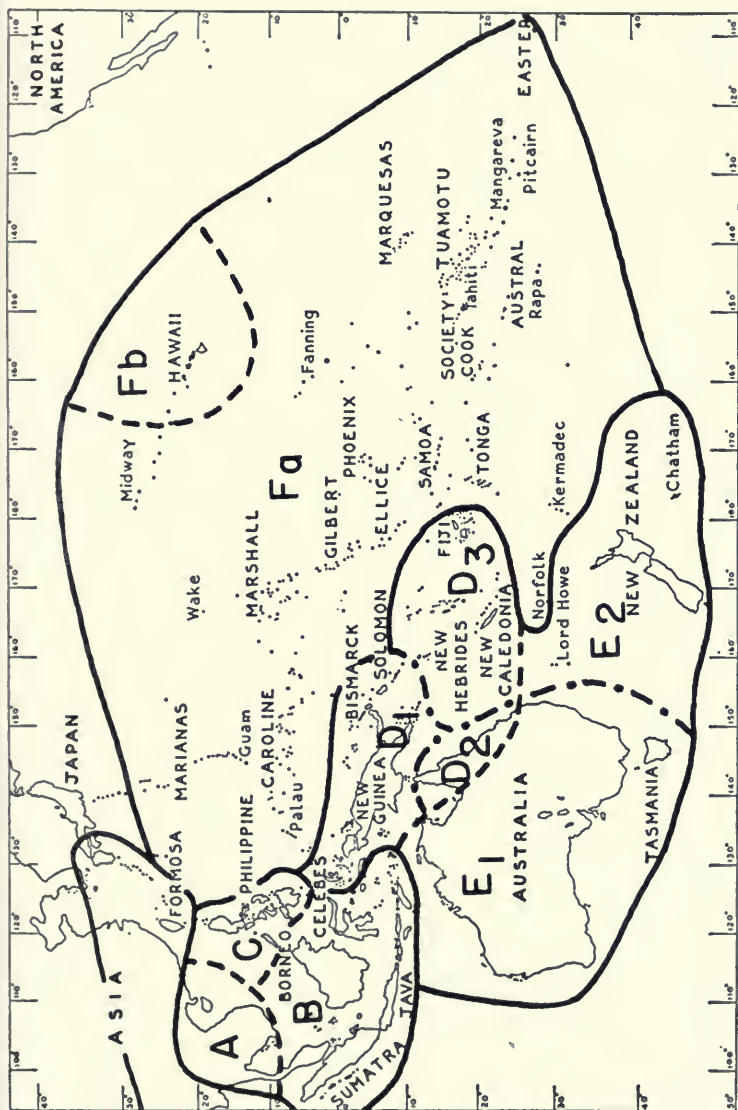


FIG. 31. Land snail regions of the Pacific Ocean (after A. H. Cooke, 1895).

ORIENTAL REGION: A, Siamese; B, Malay; C, Philippine. AUSTRALIAN: D, Papuan (1, Papuan; 2, Queensland; 3, Melanesian); E, Australian (1, New Zealand); F, Polynesian (a, Polynesian; b, Hawaiian).

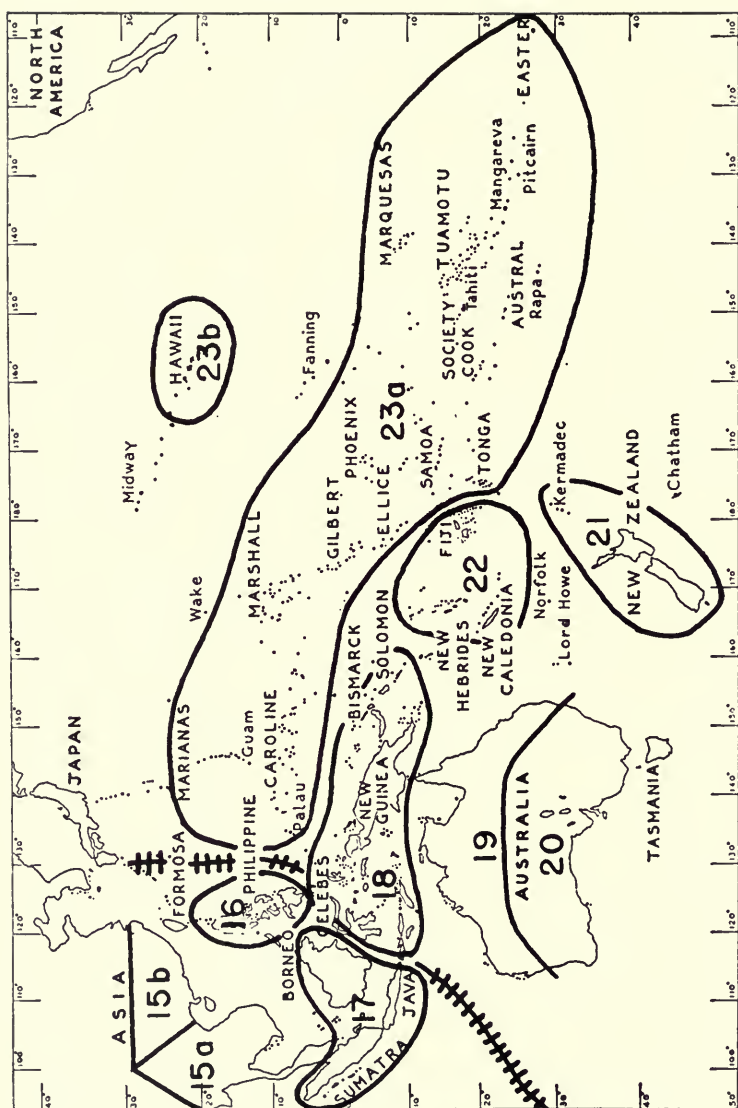


FIG. 32. Land snail regions of the Pacific Ocean (after P. H. Fischer, 1950).

PALÉOTROPICALE ORIENTALE: 15, Indo-chinoise (a, Indo-china; b, Chine méridionale); 16, Philippinienne; 17, Indo-malaise. OCEANENNE: 18, Mélanésienne; 19, Australienne tropicale; 20, Australienne tempérée; 21, Néozélandaise; 22, Néocalédonienne; 23, Polynésienne (a, à *Partula*; b, à *Achatinella*).

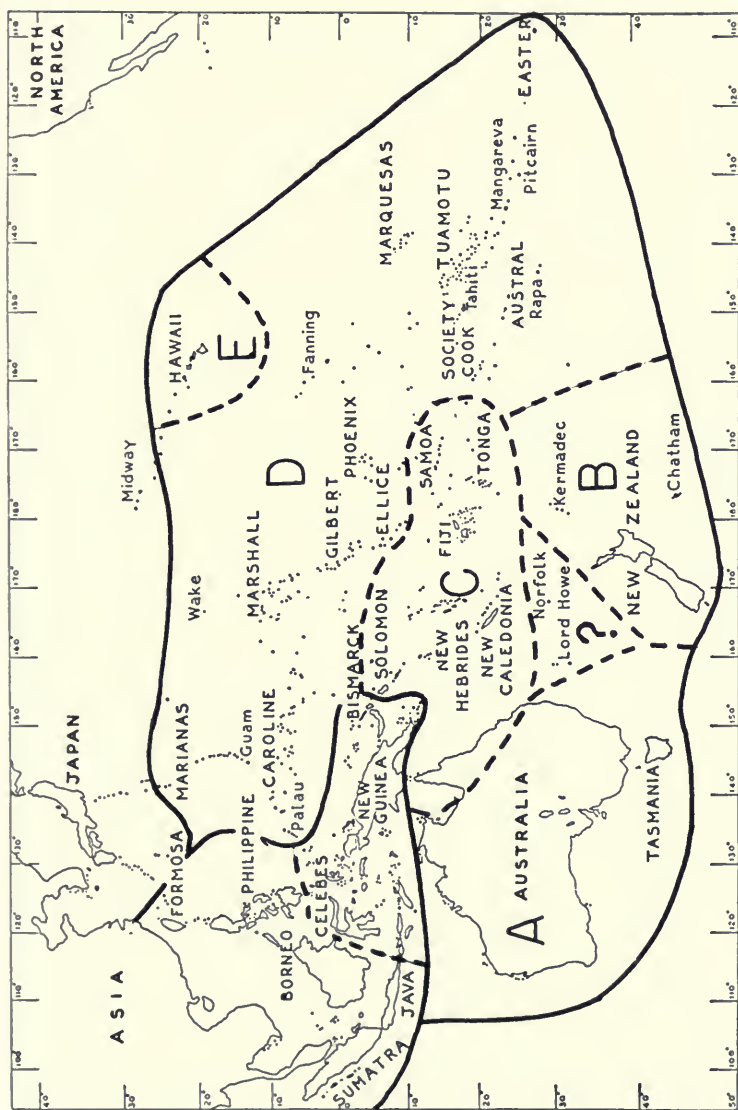


FIG. 33. Insect regions of the Pacific Ocean (after Holdhaus, 1934).

AUSTRALIAN REGION: A, Austrotasmanische; B, Neuzelandische; C, Melanesische; D, Polynésische; E, Hawaiische.

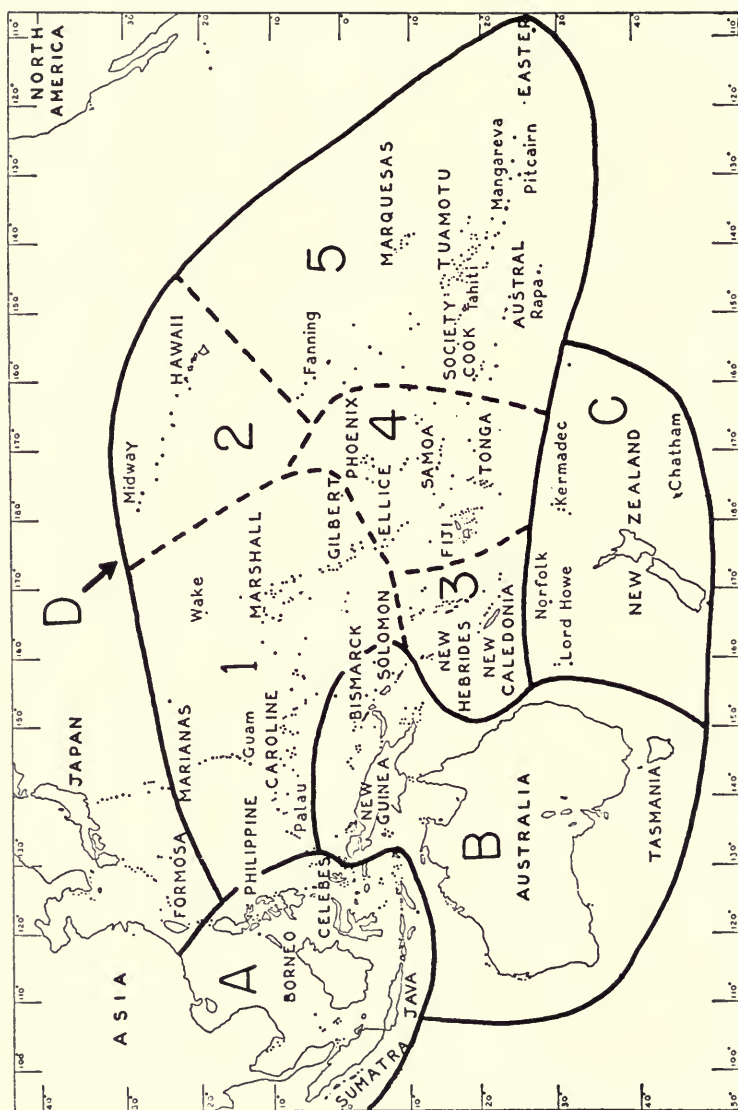


FIG. 34. Avian regions of the Pacific Ocean (after Mayr, 1940a).

A, ORIENTAL (not subdivided). B, AUSTRALIAN (not subdivided). C, NEW ZEALAND. D, POLYNESIAN: 1, Micronesian; 2, Hawaiian; 3, southern Melanesian; 4, central Polynesian; 5, eastern Polynesian.

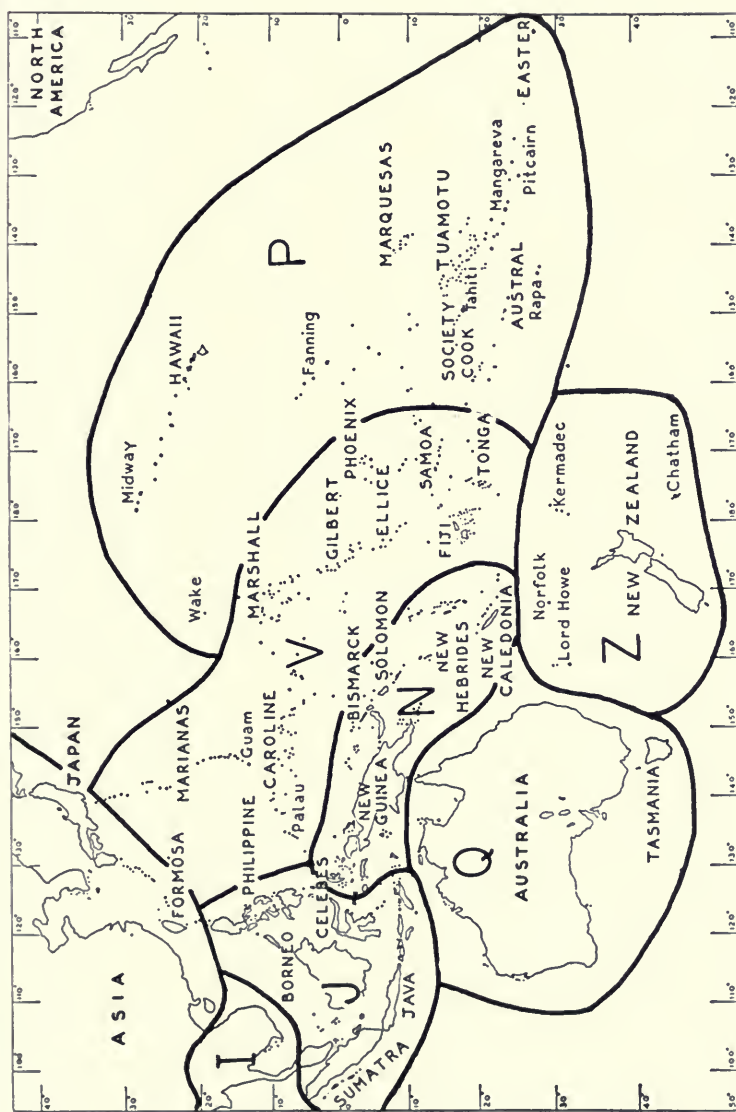


FIG. 35. Terrestrial faunal regions of the Pacific Ocean (after Schilder, 1956).

I, Südasien; J, Indonesien; N, Melanesien; P, Zentral-Pazifik; Q, Australien; V, West-Pazifik; Z, Neuseeland.

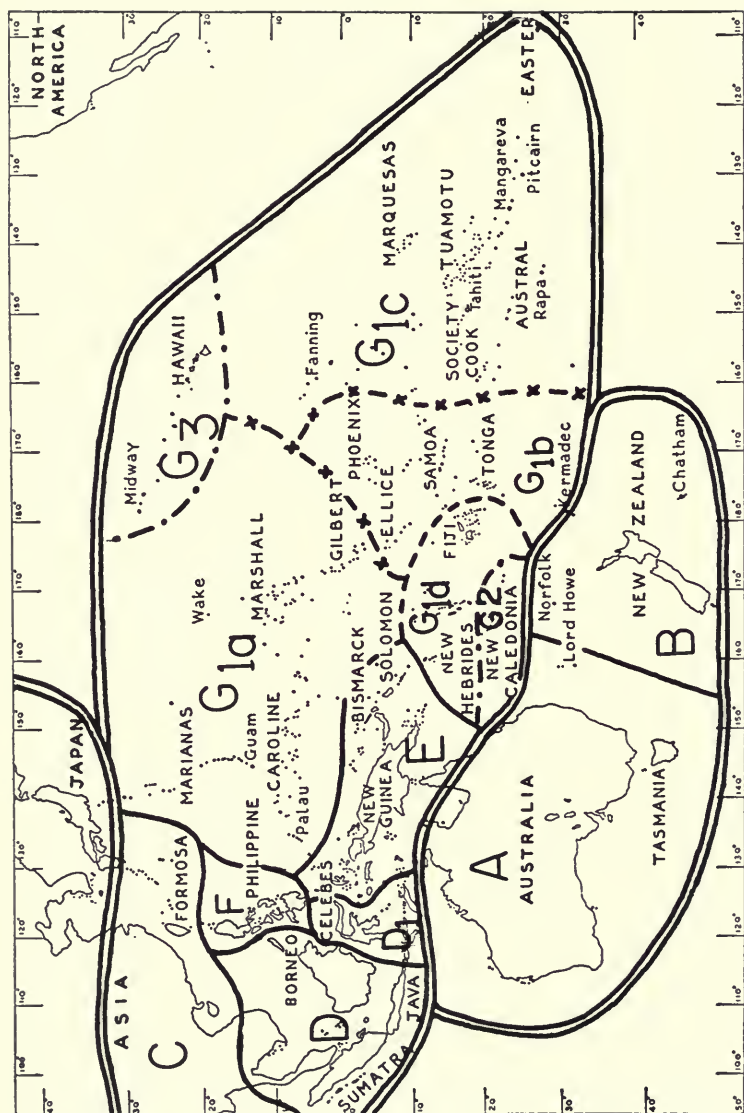


FIG. 36. Inset regions of the Pacific Ocean (after Gressitt, 1956).

AUSTRALIAN REGION: A, Australian subregion. B, New Zealand subregion. ORIENTAL REGION: C, Indo-Chinese subregion. D, Malayan subregion. D1, Celebes transition zone. E, Papuan subregion. F, Philippine subregion. G, Polynesian subregion: 1, Polynesian division (a, Micronesia; b, central Polynesia; c, southeastern Polynesia; d, eastern Melanesia); 2, New Caledonian division; 3, Hawaiian division.

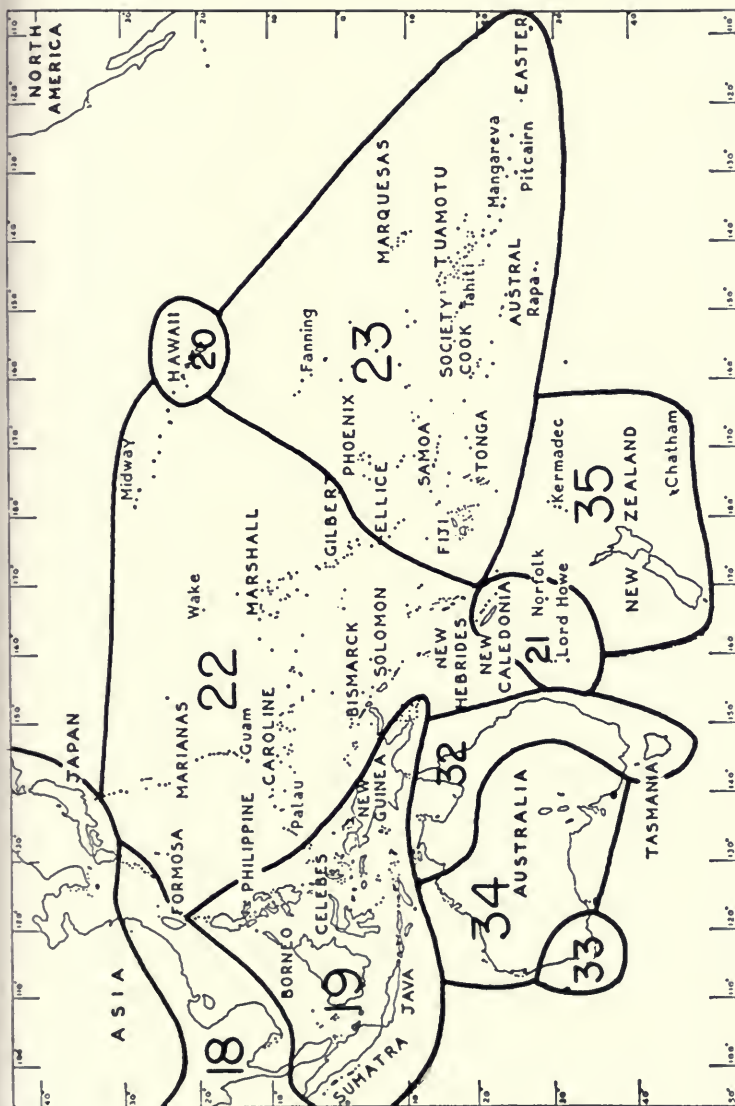


FIG. 37. Plant regions of the Pacific Ocean (after Good, 1953).

PALAEOTROPICAL KINGDOM: A, African subkingdom (not shown). B, Indo-Malaysian subkingdom: 18, continental southeast Asian; 19, Malaysian. C, Polynesian subkingdom: 20, Hawaiian; 21, New Caledonian; 22, Melanesian and Micronesian; 23, Polynesian. AUSTRALIAN KINGDOM: 32, northern and eastern Australia; 33, southwestern Australia; 34, central Australia. ANTARCTIC KINGDOM: 35, New Zealand.

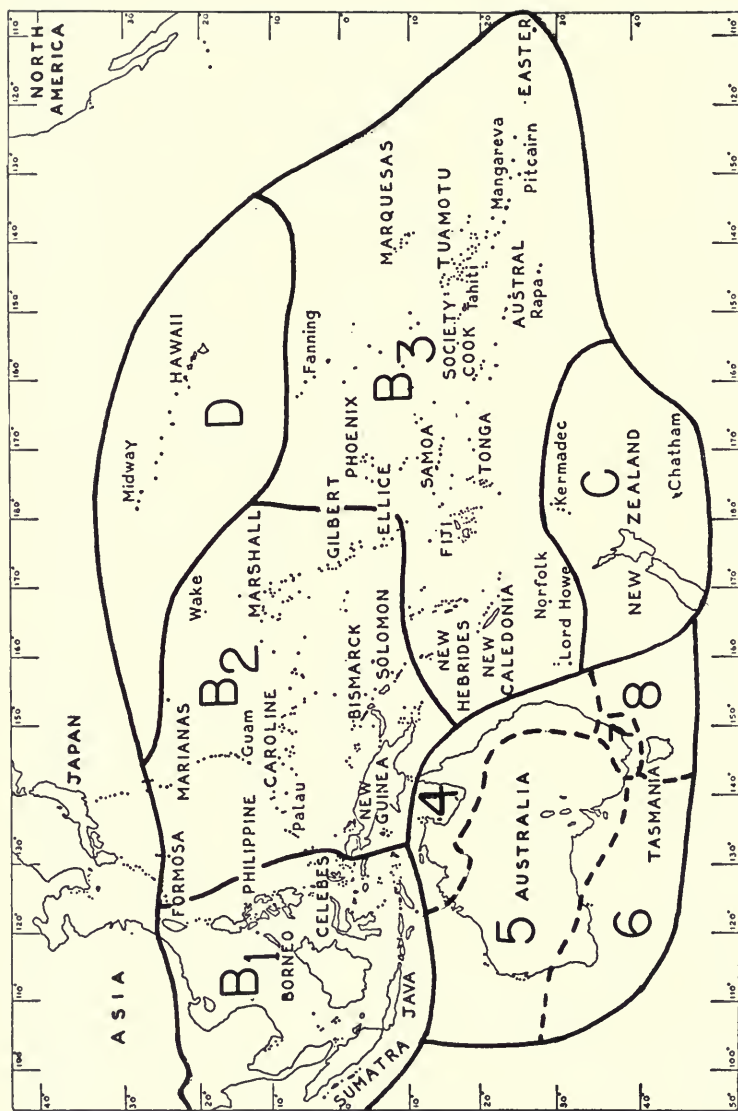


FIG. 38. Plant regions of the Pacific Ocean (after Hayek, 1926).

PALÄOTROPISCHES FLORENREICH: A, Indoafrikanisches Gebiet (not shown). B, Malayesisches Gebiet: 1, Malayische Provinz; 2, Melanesische Provinz; 3, Polynesisches Provinz. C, Neu-Seeländisches Gebiet. D, Sandwich-Inseln-Gebiet. AUSTRALISCHES FLORENREICH: 4, Nord- und Ost-Australische Provinz; 5, Eremaische Provinz; 6, West-Australische Provinz; 7, Südaustralische Hochgebirgs Provinz; 8, Tasmanische Provinz.

The occurrence of many streptaxids in the Philippines, three on Celebes, and one(?) on Borneo is surprising. The crossing from Malaya to Sumatra adds, as well as subtracts, molluscan taxa. The families Tornatellinidae (fig. 13), Assimineidae (fig. 12), Helicinidae (fig. 14), and Endodontidae are completely absent from or are barely represented on the mainland. The Omphalotropidinae, Endodontidae, and Tornatellinidae do not become important until much farther east, but the Helicinidae have undergone a minor radiation in parts of Indonesia. Relict endodontids are found in southern India and Ceylon, omphalotropids and tornatellinids on the Mascarene Islands, and omphalotropids and helicinids on the Nicobar and Andaman Islands. All these taxa seem to have been replaced on the mainland of Asia.

Between Java and New Guinea are the Lesser Sunda Islands and the Moluccas. To the north of Celebes and Borneo is the Philippine Archipelago. Many papers on the malacofauna of this area have appeared since the pioneer attempts of the Sarasin brothers. Most papers have been faunistic in scope and generic affinities are too poorly understood to allow a detailed analysis of generic distribution. Genera such as *Pterocyclus*, *Platyraphe*, and *Alycaeus* of the Cyclophoridae; *Amphidromus* (fig. 20) and *Landouria* of the Camaenidae; and *Elaphroconcha* of the Helicarionidae do stop short of New Guinea. Others in the same families, such as *Cyclotus*, *Leptopoma*, *Ditropis*, and *Lagochilus* of the Cyclophoridae; *Chloritis* (fig. 19), *Planispira*, and *Ganesella* of the Camaenidae; and the "*Hemiplecta*" types of helicarionids live on both Java and New Guinea. Smaller snails such as the Pupinidae (fig. 14), Diplommatinidae (fig. 17), several endodontids (fig. 24), and many "zonitoids" have an uninterrupted Papuan-Indonesian range (see van Benthem Jutting, 1953b).

On the *family* level, the Indonesian-Papuan affinities are even more startling. Except for the Philippine Island Streptaxidae, Strobilopsidae (fig. 18), and Fruticicolidae (*Helicostyla*, s.l., fig. 27), *no family of land snails found in any part of Indonesia is absent from New Guinea* (see figs. 12-17, 19).

Apparently the distribution patterns of the New Guinea land snails are very complex. The studies of Tapparone-Canefri (1883), Hedley (1892b), Leschke (1912), van Benthem Jutting (1933), and Iredale (1941) suggest that there are important differences between the eastern and western parts of the island. The fauna of the New Guinea interior is so poorly known, however, that any attempt to propose faunal divisions is premature. Families such as the Clau-

siliidae (fig. 14), the Enidae (fig. 16), and the Athoracophoridae (fig. 18) are recorded from only one or two localities, but probably are rather widely distributed.

The most obvious new member of the "Papuan" fauna is the camaenid genus *Papuina* (fig. 20), also known from Queensland, the Bismarcks, and the Solomons. Geographically, and probably ecologically, *Papuina* replaces *Amphidromus* (fig. 20). The change is only of generic value, however. An aberrant assimineid (*Pseudocyclotus*), a few paryphantids of Australian affinities, scattered records for the Polynesian *Partula* (fig. 12) on the far eastern tip and on the Louisiades, the relict Megaspiridae,¹ and an athoracophorid slug (*Triboniophorus*, fig. 21) provide the few non-Malayan derivations. A portion of the "Malayan" fauna dips into Australia along the Queensland coast to northern New South Wales, and the distribution charts show that many families and genera also reach the Bismarcks and the Solomons.

On the basis of mollusks, then, *there is essentially one fauna, which stretches from Java to the Solomons and northern New South Wales. The entire area is characterized by the Cyclophoridae, Camaenidae, Rathouisiidae, and larger helicarionid snails. This fauna may be termed the Palaeo-Oriental.* Groups such as the Pupinidae (fig. 14), Diplommatinidae (fig. 17), Pupillidae, Trochomorphinae (fig. 19), and Helicinidae (fig. 14) "spill over" into the Pacific; the Enidae (fig. 16) and Clausiliidae (fig. 14) are weakly represented throughout most of "Indo-Papua," while groups which include the Assimineidae (fig. 12), Tornatellinidae (fig. 13), Microcystinae (fig. 15), and Endodontidae become prominent only after passing beyond the boundaries of the Palaeo-Oriental area.

The endodontids may serve as an example of the last distribution. Three genera are found in the Philippines (Solem, 1957) and Greater Sunda Islands (see figs. 24-26). *Stenopylis* (fig. 24) has one species which ranges to the Solomons and central Australia; *Beilania* (fig. 25) has one species in Indonesia and a large radiation in Micronesia; and *Discocaropa* (fig. 24) has a few widespread species with aberrant forms in the Kermadecs, Tasmania, and Mindanao. New Guinea has an endemic genus with partially reduced shell (*Paryphantopsis*, fig. 26) and some species derived from a Moluccan type (Solem, 1958b). In contrast, Micronesia and Polynesia have many species and several endemic genera, and Australia, New Zealand, and New Caledonia

¹ A New Guinea-Queensland range, with living species in Brazil and Eocene fossils in Europe.

have a bewildering variety of endodontid genera and species (see figs. 13, 24-26).

ISLANDS OF THE PACIFIC OCEAN

On the Pacific islands there are the already mentioned radiations of endodontids (figs. 24-26), the helicarionid subfamily Microcystinae (fig. 15; see H. B. Baker, 1941, for a discussion of the zoogeography of this subfamily), the endemic family Partulidae (fig. 12), several types of helicinids (figs. 22, 23), numerous omphalotropids, and tornatellinids in many areas. The Hawaiian Islands have the endemic Amastridae and Achatinellidae (fig. 16), and many local succineids, pupillids, and tornatellinids. The "inner fringe" of islands (Palau, Carolines, New Hebrides, and Fijis) have varying numbers of Palaeo-Oriental genera, and, surprisingly, some endemic taxa: *Dendrotrochus* (a sesarine helicarionid, fig. 19), a subgenus of the rhytidid genus *Delos* (*Hebridelos*, fig. 28), and the cyclophoraceid family Poteriidae (fig. 16), otherwise found only in Central America and the West Indies. The Melanesian islands have complicating factors and are not mentioned at this time. Unlike the situation found in other phyla, the Pacific islands have a land snail fauna which is highly endemic and, although probably derived from the Palaeo-Oriental region, now forms a distinct entity. *This will hereafter be referred to as the Pacific Island fauna.*

At this point it should be emphasized that "... The land snails of the Pacific islands, as far as now known, may be divided into two groups: those living on low islands and on the shore zones of high islands, and those inhabiting the forests of high islands. Many of the first group have a wide distribution suggestive of dispersal by human or other adventitious agency and are therefore not significant in the present problem." (Pilsbry, 1916, p. 429; see also C. M. Cooke, 1926, pp. 2278-79.) The land snails of the forest zones on high islands are almost entirely endemic and limited to single islands or archipelagos. In speaking of a Pacific Island faunal element, it is the high island forest snails that are referred to and not the "atoll fauna."

AUSTRALIA, NEW ZEALAND, AND NEW CALEDONIA

Australia, New Zealand, and New Caledonia show one great faunal similarity: each area has an extremely extensive radiation of the Paryphantidae and Endodontidae. Endodontids are found on the Pacific islands, but the subfamily Punctinae (fig. 13) and the

"Flammulinidae" (fig. 13) of Suter and Iredale are almost exclusively a New Zealand-New Caledonian-Australian development. Present in Australia, but not in the other two, are many endemic camaenids (the Hadridae, Xanthomelonidae, and Rhagadidae of Iredale; fig. 17), the mesurethran relict Caryodidae (fig. 12), and the bulimulid *Bothriembryon* (fig. 20). New Caledonia and New Zealand have *Placostylus* (fig. 20) and athoracophorid slugs (fig. 21). The latter are present in part of Australia, but do not form an important element. The Caryodinae and Camaenidae of Australia represent geologically (and phylogenetically) more recent elements than the Paryphantidae, Bulimulidae and Endodontidae. Their presence in Australia does not alter the essential homogeneity of the Australian, New Zealand and New Caledonian snail fauna. *This distinctive assemblage may be called the Southern Relict fauna.* The chosen name deliberately implies South African and South American associations, although a "world wide snail geography" cannot be presented at this time.

SUMMARY

There are three main faunal assemblages of land snails in the Indo-Pacific region. These are called the Palaeo-Oriental, Pacific Island, and Southern Relict faunas. All three intermingle on the islands of Melanesia. Delimitation of faunal regions and any comments on the origin of the faunas must be based on a detailed analysis of the snails found on the Melanesian Islands.

Faunas of Particular Areas

The tabular comparisons (Tables XVI and XVII and figs. 7 and 8, no. 1, this volume) and range maps (figs. 12-28) provide the basic data but are supplemented by a detailed comparison of the New Hebridean snail fauna with that found in other areas. Only after this is an attempt made to recognize major faunal regions.

BISMARCK ARCHIPELAGO, INCLUDING THE ADMIRALTY ISLANDS

A few large helicarionids (*Nesonanina*, "*Hemiplecta*"), *Philalanka*, *Leptopoma*, *Lagochilus* (see I. Rensch, 1937, p. 605), *Chloritis*, and the Rathousiidae are continuing Palaeo-Oriental taxa, but *Cyclotus*, and *Planispira* of Indonesia and Papua are absent. There is an increased number of Trochomorphinae (including the endemic *Coxia*), Endodontidae, and Omphalotropidinae. *Partula* (a Pacific Island taxon) is prominent for the first time. The sesarine *Dendrotrochus*

makes its first appearance, there is an advanced athoracophorid (*Aneitella*), and an extensive series of *Papuina* (see I. Rensch, 1934a). Although there is little affinity with New Guinea on the species level (I. Rensch, 1937, p. 643), and there is an intrusion of Pacific Island forms such as *Partula*, *Cyclomorpha*, and *Omphalotropis*, the major portion of the fauna is Malayan or Papuan (*Papuina*, *Pseudocyclotus*, *Palaeohelicina*).

SOLOMON ISLANDS

The Solomons represent the last important outpost of the Palaeo-Oriental fauna. *Chloritis*, *Leptopoma*, *Stenopylis*, a unionid mussel (*Leiovirgus guppyi* E. A. Smith), and two "*Helicarion*" are purely Malayan, while *Papuina*, *Pseudocyclotus*, and *Palaeohelicina* are "Papuan" genera and *Cryptaegis*, *Crystallopsis*, and *Setaepoma* are endemic derivatives of Papuan taxa.

From the Pacific Islands comes *Partula*, and from the Southern Relict fauna *Placostylus*. The Solomon Island *Placostylus* are closely related to the Fijian, and only slightly to the New Hebridean (fig. 20). Minute helicarionids, athoracophorid slugs, and rathouisiid slugs are not yet known from the Solomons, but probably they occur there.

In comparison with the New Hebrides, the Solomons lack *Delos*, *Draparnaudia*, most of the Endodontidae, and the Poteriidae. Among the genera found in both the New Hebrides and the Solomons, *Papusuccinea*, *Macrocyloides*, *Mocella*, *Partula*, and *Palaina* are characteristic of wide areas and do not indicate any special affinities. The Solomon Island *Ouagapia* is more closely related to the New Caledonian than the New Hebridean species. *Dendrotrochus*, *Orpiella*, *Trochomorpha*, *Pupina*, and *Omphalotropis* have distinct subgeneric units in the New Hebrides. Although only eight New Hebridean genera are absent from the Solomons, the similarities are caused by the general mixing of faunal elements in Melanesia or by very widely distributed taxa. No genera indicate a direct, close relationship between the snail faunas of the Solomons and New Hebrides. Clapp (1923), I. and B. Rensch (1935, 1936), and Clench (1941) cite a few specific distributions as including both the Solomons and the New Hebrides, but these are all based on erroneous data in previous publications.

NEW CALEDONIA AND LOYALTY ISLANDS

Gassies (1863, 1871, 1880), Crosse (1894), Dautzenberg (1923), and Franc (1957) summarized the New Caledonian snail fauna.

Franc did an excellent job of taxonomy on the species level, but his classification was taken completely from earlier works. On the basis of studies made during this investigation, I had started a reclassification of the New Caledonian land snails. Franc's excellent revisions of species enabled me to prepare a classified check list of New Caledonian non-marine snails (Solem, in press) in which the generic and familial classification is correlated with the systematic conclusions outlined (no. 1, this volume). The following synopsis of the fauna is taken from Solem (in press).

New Caledonia lacks the Pupinidae (fig. 14), Partulidae (fig. 12), Helicarionidae (fig. 15),¹ and Zonitidae (fig. 19)¹ which are native to the New Hebrides. Of the about 153 endemic species of land snails found in New Caledonia, 73 per cent belong to the Bulimulidae, Endodontidae, and Paryphantidae. There are only a very few succineids, tornatellinids, diplommatinids, omphalotropids, and heliciniids (few *species* although many *names*) when compared to the Pacific Ocean or Palaeo-Oriental faunas. In over-all facies, the New Caledonian fauna is the same as that of New Zealand and southern Australia.

The New Caledonian Bulimulidae (*Placostylus*) are intermediate between those of the New Hebrides and the Solomons (see pp. 128-129, no. 1, this volume). The New Caledonian Paryphantidae include a Papuan genus (*Ouagapia*); one of New Zealand and East Australian affinities (*Ptychorhytida*); and two endemics (*Diplomphalus* and *Microphyura*).

The position of the New Caledonian Endodontidae is difficult to determine in the absence of anatomical data. All genera appear to be endemic, but they are most closely related to Australian-New Zealand genera. The New Caledonian genera with spiral apical sculpture are similar to *Mocella* (see p. 79, no. 1, this volume) but probably represent a more advanced stock, since the sculpture is finer. A similar situation is seen in the Micronesian *Beilania*. The Mariana species have simple shells with coarse apical sculpture while the Palau and Caroline species have modified shells and much finer apical sculpture. Since *Mocella* (fig. 25) has a fringe distribution around the finer-sculptured New Caledonian-East Australian genera (fig. 25), it can be assumed for a working hypothesis that few prominent lirae are primitive and many fine ones advanced. The New Caledonian genera with radial apical sculpture or reduced sculpture

¹ Franc (1957, pp. 144-150) listed several New Caledonian "limacoid" species. They are all either introduced, cannot be presently referred to a family group, or may be one native group (*Orpiella*) (Solem, in press).

(*Platyrhytida*, *Pararhytida*) resemble some Australian-New Zealand genera, but their exact affinities are unknown. They have been referred to the "Flammulinidae," which, except for one Caroline Island species (see Moellendorff, 1900), are exclusively Southern Relict elements.

The closest affinities of the New Caledonian and New Hebridean fauna are shown by the athoracophorid slug genus *Aneitea* (fig. 21) and the small sinistral snail *Draparnaudia* (fig. 17). Both are restricted to the two areas. *Aneitea* is intermediate between the New Zealand *Athoracophorus* and the Bismarek *Aneitella* and is similar to, but probably not closely related to, the Austral-New Guinean *Triboniophorus* (see pp. 45, 46, no. 1, this volume). *Draparnaudia* is of unknown family affinity. On the basis of distribution and conchological similarities, it *may* be a toothless tornatellinid (see p. 121, op. cit.), but its anatomy is insufficiently known to enable placement in a family.

Pleuropoma may have a section endemic to New Caledonia and the New Hebrides; the Poteriidae have *Gonatoraphe* in the New Hebrides and *Gassiesia* in New Caledonia; and the *Placostylus* of New Caledonia are intermediate between the New Hebridean and Solomon Island species. The New Hebridean *Placostylus* are more closely related to the species from New Zealand and Lord Howe Island than to those of New Caledonia (fig. 20).

Of the other genera found in both areas, *Palaina* and *Papusuccinea* are widely distributed; *Ouagapia* (fig. 27) shows both Solomon Island and New Hebridean type species; and the species of *Omphalotropis* will probably be placed in different genera.

Since New Caledonia is the land mass nearest to the New Hebrides, and winds, currents, and storms favor dispersal from the New Hebrides to New Caledonia, the differences between the two areas are very important. The Partulidae and Limacacea managed to reach some of the farthest oceanic islands of the Pacific. Their failure to pass the relatively narrow water gap between the southern New Hebrides and New Caledonia is highly significant zoogeographically. Apparently there is no climatic or floristic explanation. The climates are the same, and Guillaumin (1926, pp. 29-30) considered that the floras were nearly identical. Later, however, Guillaumin (1934a; 1934b, pp. 261, 264-265; 1953, p. 121) placed the New Hebrides in a separate subregion from New Caledonia, but this separation was based on an analysis of the *entire* island chain, rather than only the southern islands. It might be argued that the endodontids and rhy-

tidids would effectively bar colonization by "zonitids," but carnivorous snails have not eliminated them elsewhere. The zonitids consistently have replaced the endodontids on continental areas, and introduced zonitids have flourished in New Caledonia.

Sixteen genera (64 per cent) of the New Hebridean land snails are absent from New Caledonia. This ratio compares with only eight (32 per cent) New Hebridean genera absent from the Solomon Islands and Fiji, both of which are more than twice as far away.

The situation is different with regard to the fresh-water snails. Both New Hebridean planorbids live in New Caledonia. This similarity between the New Hebrides and New Caledonia probably results from the much greater dispersal powers possessed by fresh-water mollusks in comparison with land snails. Neither area has fresh-water mussels, but this is characteristic of all Pacific islands except the Solomons and New Zealand.

LORD HOWE ISLAND

Iredale (1944) obscured the relationships of the Lord Howe Island land snails by burying them under new generic and family names. When these nomenclatural associations are ignored the fauna shows diverse affinities (based on the original material of Preston in the UMMZ). The *Placostylus* hardly differ from the New Zealand species in sculpture, the endodontids seem close to several New Zealand types, with one (*Hedleyoconcha*) Australian type, while the various "zonitids" have east Australian relatives (see H. B. Baker, 1941, p. 264). The fauna thus has an "ancient" New Zealand element, and a "modern" Australian one (see also Iredale and Allan, 1940).

NORFOLK ISLAND

Iredale (1945) provided many names for the Norfolk Island shells. Study of specimens suggests that they are quite different from the types found on Lord Howe Island and probably were derived from Polynesian ancestors. This is the same conclusion earlier reached by Iredale (1915).

KERMADEC ISLANDS

Much valuable information was offered by Iredale (1913, 1915), who pointed out biological data about the species and carefully described and figured the many new forms. His conclusion that a few New Zealand elements are present and that others were derived by drift or by way of the Polynesians is probably correct.

NEW ZEALAND

The New Zealand land snails (Powell, 1946a) consist of 262 species placed in 43 genera. The Endodontidae (Flammulinidae, Charopidae, Laomidae, Otoconchidae) have 183 species (70.5 per cent) in 23 genera (57.5 per cent), the Paryphantidae 39 species (15.2 per cent) in 5 genera (12.5 per cent). Three *Placostylus*, ten *Athoracophorus*, four *Liarea* (= *Realia*), fourteen *Murdochia*, two tornatellinids, one *Papusuccinea*, one *Hydrocena*, two assimineids, and one "zonitoid" snail¹ complete the fauna.

Liarea has been referred to the Malayan Pupinidae, but the heavily sculptured shell is completely different and the radula (Powell, 1954, pl. 48, figs. 38–40) is not the pupinid type. The family relations of *Murdochia* are uncertain. Morton (1952) showed that it is a cyclophoracean, but no family designation is possible. The two tornatellinids, the hydrocenid, and the assimineids could have been introduced by the Polynesians or (if truly endemic) derived from drift, since all the genera are widely distributed on the outer islands of the Pacific. The "zonitoid" snail, "*Suturella*," is the only disharmonic element in the fauna, but it is of unknown affinity and possibly is introduced.

Of the families found in New Caledonia, only the Helicinidae is absent from New Zealand, yet there are no important generic affinities between New Zealand and New Caledonia. *Placostylus* (fig. 20) and *Rhytida* (fig. 28) have different subgenera in the two islands, and only the widely distributed *Papusuccinea* is common to both.

It is astonishing to find direct relationships between the faunas of the New Hebrides and New Zealand. Besides *Papusuccinea*, *Mocella* (fig. 25) and *Delos* (fig. 28) are found in both places, and there are two taxa—*Phrixgnathus* (fig. 26) and *Placostylus*, s. s. (fig. 20)—found *only* in New Zealand and the New Hebrides. *Phrixgnathus* has no obvious relatives elsewhere, but *Placostylus* is represented by different subgenera on New Caledonia, Fiji, and the Solomons. I am not aware that similar relationships have been found in other phyla.

The fresh-water fauna of New Zealand is remarkable for the presence of a few highly variable mussels, tentatively referred to *Hyridella* (see Dell, 1953, and McMichael, 1958). Fossil unionids are known from the Upper Cretaceous of New Zealand (McMichael, 1957), but these do not seem to be ancestral to the Recent species (McMichael,

¹ Dell (1952b) has shown that the two "*Helicarion*" reported by Powell (1946a) are related to *Otoconcha* and are thus local arionaceans not related to the limacacean family Helicarionidae.

1958, p. 429). McMichael would derive the New Zealand mussels from Australia in comparatively recent times by accidental transport on birds' feet. McMichael and Hiscock (1958, p. 496) suggest that all recent and fossil New Zealand mussels could be accounted for by five accidental introductions ranging from the Upper Cretaceous to the late Tertiary.

FIJI ISLANDS

Fiji (Germain, 1932; H. B. Baker, 1938b, 1941) has *Trochomorpha*, *Palaina*, and *Pupina* of the Palaeo-Oriental fauna, *Orpiella* and *Ouagapia* (fig. 27) of Papuan origin, and *Placostylus* (fig. 20), the species of which are very closely related to those of the Solomons. Otherwise the fauna is Pacific Ocean in character.

In comparison with the New Hebrides, the Fijis have a more extensive radiation of heliciniids and *Omphalotropis*, fewer kinds of endodontids, and many more minute "zonitids." The Fijis lack *Papusuccinea*, *Dendrotrochus* (fig. 19), *Draparnaudia* (fig. 17), *Macrocyclodes* (fig. 27), the New Hebridean endodont genera (except *Mocella*), and the Athoracophoridae (fig. 21). Both areas have *Partula*, *Mocella* (fig. 25), *Ouagapia* (fig. 27), and *Palaina* of the wide-ranging genera; different subgenera of *Diastole*, *Lamprocystis*, *Orpiella*, *Trochomorpha*, *Placostylus* (fig. 20), *Pleuropoma* (fig. 22), *Pupina*, and *Omphalotropis*; and two generic units restricted to the areas, *Hebridelos* and *Gonatoraphe*. *Hebridelos* is also found in the Caroline Islands, but *Gonatoraphe* is only in Fiji and the New Hebrides. Derivatives from *Gonatoraphe* are found in New Caledonia and Samoa.

The absence of Camaenidae, Rathouisiidae (fig. 17), and Cyclophoridae (fig. 16) tends to make recent continental connections unlikely, but, as indicated below, the presence of *Placostylus* would seem to demand some land connections in the past (see Woolnough, 1903).

TONGA

The fauna of Tonga (Mousson, 1871; H. B. Baker, 1938b, 1941) is distinctly oceanic, containing *Partula*, *Samoana*, *Mocella*, Microcystinae, Heliciniidae, Assimineidae, Tornatellinidae and one *Papusuccinea*. There are a few relicts from the Palaeo-Oriental fauna—*Ouagapia* (fig. 27), *Palaina*, and *Trochomorpha* (fig. 19). Samoa has *Ouagapia* and *Trochomorpha* and the poteriid genus *Ostodes*. *Trochomorpha* continues eastward to the Society Islands. This is obviously only an attenuation of the Palaeo-Oriental element.

Tonga, Samoa, and the more eastern islands all lack the Pupiniidae, *Hebridelos*, and *Placostylus* of Fiji and the New Hebrides.

CAROLINE ISLANDS

The land snails of the Caroline Islands (Moellendorff, 1900; H. B. Baker, 1938b, 1941) show close relationship to the New Hebridean taxa in having only *Hebridelos* (fig. 28), a different subgenus of *Dendrotrachus* (fig. 19), and some Poteriidae (fig. 16). The Partulidae, *Omphalotropis*, Tornatellinidae, *Pupina*, *Pleuropoma*, and *Trochomorpha* complete the resemblance.

The Caroline Islands differ in having a *Ryssota* on Truk, endemic species of *Beilania*, the helicinid *Sturanyella*, and three endemic genera of Trochomorphinae (*Hogolua*, *Kondoa*, and *Brazieria*). In speaking of the fauna of the Carolines it might be more appropriate to speak only of Truk, Kusaie, Lukonor, and Ponape, since these four islands contain almost all of the endemic elements.

PALAU ISLANDS

The Palaus have no special affinities with the New Hebrides but are worth mentioning because of the remarkable radiation of the trochomorphid genus *Videna*, which occurred there, and the presence of derivatives of *Beilania*, several partulids, the microcystine *Palaua*, and some *Palaeohelicina*.

The Micronesian islands of Palau and the Carolines have a fauna with an extraordinary amount of evolution on the *generic level*. The taxa represented on Palau and the Carolines—Endodontidae, Zonitidae, and Partulidae—show more profound structural divergences in these islands than on all the rest of the Oceanic islands combined. Speciation has been comparatively slight, particularly when compared with that on Hawaii or the Society Islands, but generic differentiation has been enormous. Whether this indicates multiple introductions from Indonesia, relicts from a larger land mass crowded into the small islands by the sinking ocean bed of Micronesia, or another cause, is unknown.

AUSTRALIA

The land and fresh-water mollusks of Australia have been summarized in checklists by Iredale (1937a,b, 1938, 1943b). These documents are remarkable not only for the vast amount of compilation involved, but also for the incredible number of new generic and

family units established. To make meaningful comparisons with the other areas it has been necessary to "downgrade" the great majority of Iredale's families and many of his genera (see pp. 28-29, no. 1, this volume).

Iredale (1937a, pp. 287-290) divided Australia into several zoogeographic provinces based on the land snail distribution. Much of his information was derived from Hedley (1899). The coastal areas of Queensland and northern New South Wales have a New Guinean fauna, with *Papuina* (fig. 20), *Chloritis* (fig. 19), a few Cyclophoridae (fig. 16), Rathouisiidae (fig. 17), Pupinellinae, the athoracophorid *Triboniophorus* (fig. 21), a subgenus of *Pupina*, one species of Enidae (fig. 16), and the majority of the Australian shell-bearing Helicari-onidae (fig. 15). There are very few endodontids, but many large camaenids.

Several authors suggested that a close relationship exists between Queensland and the New Hebrides-New Caledonian region. The insects (Chopard, 1934, p. 186; Holdhaus, 1934, p. 210; but see also Gressitt, 1956, p. 14), spiders (Berland, 1934, p. 156; 1938), and plants (Guillaumin, 1934b, pp. 264-265; 1953, p. 121) all have Queensland-southern Melanesian taxa. Very few are found in the land mollusks. *Pupina* (fig. 14), and *Discocharopa* (fig. 24) are Palaeo-Oriental in origin; *Delos* (fig. 28) has different subgenera; and the Athoracophoridae has different genera. Otherwise there are no Queensland-New Hebridean affinities. The New Caledonian-Queensland tie is stronger, with some endodontids (see p. 298) and possibly a paryphantid, *Ptychorhytida*. This may not indicate a close geographic affinity; probably both received taxa via New Guinea.

In New South Wales, Victoria, and Tasmania the Palaeo-Oriental fauna is absent. In its place is a great radiation of endodontids and paryphantids, a reduced number of camaenids (*Annakelea* and *Meridolum*), and the relict family Caryodidae. The latter is a family (or subfamily) of the Acavacea, but Iredale (1937b, pp. 14-19) placed the thirteen species in four families with seven genera. Forming a transition between the southern Peronian area and Queensland Solanderian regions (Iredale, 1937a, p. 289) is the Oxleyan sub-area, with its concentration of *Hedleyella* (= *Panda*), *Pedinogyra*, and *Annakelea*.

The Centralian region has many camaenids, but little else. Similarly, the northwestern Caurine faunule has primarily desert camaenids.

Important for this study is the fauna of southwest Australia, which has the bulimulid *Bothriembryon* and several endodontids.

Only three genera of bulimulids are found in the Pacific: *Placostylus* (fig. 20), *Bothriembryon* (fig. 20), and the New Hebridean endemic, *Diplomorpha*. One species of *Bothriembryon* is found in Tasmania, but the rest are crowded into the southwest corner of Australia (Iredale, 1939, pp. 14-36, 75). Some of the southwest Australian endodontids which Iredale placed in *Luinodiscus* cannot be distinguished in shell characters from *Mocella* (fig. 25).

If Australia is considered as an isolated unit, the zoogeographic divisions of Iredale could hardly be improved on. When it is considered in relation to the rest of the Pacific, the essential similarity of the faunal elements justifies the scheme I am now proposing. In possessing pupillids, the Caryodidae and endemic camaenids, Australia shows important differences from New Zealand and New Caledonia. Nevertheless, the possession of dominating radiations of paryphantids and endodonts seems to me to be more important than those differences. The basic similarities are probably the result of an early adaptive radiation, while the differences are of more recent origin.

The relationship between the southwest portion of Australia and the New Hebrides is very tenuous, being based on *Mocella* and the Bulimulidae, but it is nonetheless significant that *any* relationship should exist between the areas, particularly since the New Hebrides and southeastern Australia show *no* relationship.

LAND SNAIL REGIONS OF INDO-PACIFIC AREA

The land snails of the Pacific show three main types of distribution (fig. 29), the Palaeo-Oriental, the Southern Relict, and the Pacific Island.¹ The Palaeo-Oriental fauna extends almost unchanged from southeastern Asia and the Malay peninsula to the Solomon Islands. In the west, a few Indian, Chinese, and Holarctic taxa intrude into Malaya, Thailand, and Burma with an unexpected recurrence in the Philippines (i.e., Streptaxidae, fig. 12; Fruticicolidae; and Strobilopsidae, fig. 18). To the east, *Partula* (Pacific Island, fig. 12) and *Placostylus* (Southern Relict, fig. 20) are present to a limited extent.

Palaeo-Oriental Subdivisions

The Philippines have peculiar elements such as *Obba* (fig. 28), Fruticicolidae (*Helicostyla*, fig. 27), Streptaxidae (fig. 12), and the

¹ Recognition of land snail "realms, regions, and provinces" should be based on a world-wide survey. Omission of the exact rank of the divisions proposed here is intentional.

Strobilopsidae (*Enteroplax*). New Guinea has a few taxa—*Papuina* (fig. 20), *Pseudocyclotus*, *Palaeohelicina* (fig. 23)—which are absent from Indonesia. Many taxa—*Leptopoma*, *Chloritis* (fig. 19), Pupinidae (fig. 14), Rathouisiidae (fig. 17), and the larger helicarionids (fig. 15)—have a continuous distribution from Java to New Guinea. Others—*Cyclophorus*, *Alycaeus*, *Amphidromus* (fig. 20)—characterize southeastern Asia, the Philippines, and most of Indonesia, but not New Guinea. There are even taxa of Philippine and New Guinea, but not Indonesian, distribution—*Ceratopoma* (fig. 22), and the subfamily Sesarinae, especially the *Inozonites*–*Zagmena*–*Theskelomensor* series (see Solem, 1958a).

Many intriguing similarities exist between the molluscan distributions shown here and the patterns for the Cerambycidae and Chrysomelidae charted by Gressitt (1956). There can be little doubt that the distribution of invertebrates within the "Palaeo-Oriental" area is much more complex than that of the vertebrates and probably has little or no correlation with the factors that produced most of the vertebrate ranges.

In view of the complicated types of distribution and over-all similarity of the fauna, no subdivisions are formally recognized at this time. "Papuan" (Aru, New Guinea, Queensland, Bismarcks, Solomons), "Indonesian" (Greater and Lesser Sunda Islands, Celebes, Moluccas), "Philippine," and "Indo-Chinese" (Malay Peninsula, Thailand, Indo-China) subareas would seem most logical, but much more careful analysis is needed.

Southern Relict Subdivisions

The range of the Southern Relict fauna includes Australia (exclusive of coastal Queensland), New Zealand, New Caledonia, and possibly Lord Howe Island. The Endodontidae and Paryphantidae are diagnostic, with the Bulimulidae, Caryodidae, and Athoracophoridae representing additional elements. The Australian Camaenidae are an extraneous taxon, reflecting the ability of camaenids to adapt to xeric conditions. Apparently the central and northwest portions of Australia represent a distinct molluscan province with only desert Camaenidae. Few faunal elements from the Palaeo-Oriental fauna have entered the Southern Relict region. *Cystopelta* and *Helicarion* probably are phylogenetically modern additions to the Australian fauna. Their presence, however, does not alter its essential homogeneity. It might here be emphasized that the family Endodontidae of the Southern Relict fauna contains not only relatives of

the Pacific Island Endodontidae, but also the Flammulinidae and Laomidae (=Punctinae) of Iredale, both of which are restricted to the area, except for a supposed *Flammulina* from the Carolines (see Moellendorff, 1900) and a *Laoma* from New Guinea (see Iredale, 1941, pp. 64–65). Possible subregions are indicated on the map (fig. 29), but recognition of these must await systematic monographs of the Endodontidae and Paryphantidae.

Pacific Island Subdivisions

The Pacific Island fauna inhabits all the islands in the Pacific Ocean from Palau and the Marianas to Hawaii and Easter Island. The Tornatellinidae are ubiquitous, the Endodontidae and Heliciniidae only slightly less so, and the Partulidae are on all high islands except Hawaii, Truk, and Easter.

The peripheral islands—Hawaii (Caum, 1928; H. B. Baker, 1940), the Marquesas (Adamson, 1939; H. B. Baker, 1941, pp. 357–358), the Society Islands (Crampton, 1916, 1932), and the Marianas (Abbott, 1949, pp. 261, 263)—have a fauna characterized by *many* species of a *few* genera. In contrast, the Palaus, the Carolines, the Fijis, and the New Hebrides have much greater generic and much less specific differentiation. An unbalanced fauna of a few taxa with much specific radiation is characteristic of a faunistically “oceanic” island; the presence of many generic and family units with only slight specific radiation is indicative of a “continental” island.

The inner fringe of islands around the Indo-New Guinea core (Palaus, Carolines, Fijis, and New Hebrides) has several genera and families not found in the more distant islands. There are perhaps four types of distribution:

(1) Taxa endemic or nearly endemic to the fringe islands: *Dendrotrachus* (fig. 19), *Hebridelos* (fig. 28), and the Poteriidae (fig. 16).

(2) Taxa present in Indonesia and extending into both Micronesia and the fringe islands of Melanesia: the Pupinidae (fig. 14), the Diplommatinidae (fig. 17) and the Trochomorphinae (fig. 19).

(3) Taxa extending only into Micronesia: *Palaeohelicina*, *Beilania* (fig. 25), and several primitive Trochomorphinae (H. B. Baker, 1941, pp. 352–354).

(4) Taxa extending only into Melanesia: *Orpiella*, *Papusuccinea*, *Ouagapia* (fig. 27) and *Fluviopupa*.

In addition to the above, the fringe islands also have the families characteristic of the outer islands.

Exceptions to the above outline do occur, but they are only minor deviations from the general pattern. The Diplommatinidae (fig. 17) reach the Marianas and Tonga; *Ouagapia* (fig. 27), Tonga and Samoa; the Poteriidae (fig. 16), Samoa (*Ostodes*); and *Trochomorpha*, Samoa, Tonga, and the Society Islands.

Subdividing the Pacific Island fauna is difficult. Hawaii is obviously a distinct subregion, but any other divisions depend entirely on which taxa are considered most important. Perhaps recognition of only two other general regions is warranted—a Transition zone of the Palaus, Carolines, Fijis, New Hebrides, and Norfolk Island and an Oceanian zone with the remaining archipelagos. Samoa and Tonga are intermediate but can be included in the Oceanian province. Further study may suggest dividing the Transition region into Micronesian (Palaus and Carolines) and Melanesian (New Hebrides, Fiji, Norfolk) provinces.

Boundaries

The transition zones between the three major faunas are relatively limited. In New South Wales there is the "Oxleyan" overlap of the Palaeo-Oriental and Southern Relict faunas, and most of Melanesia is a complex mixture of all three major faunas. Since the distinctions between the Solomons, New Hebrides, and New Caledonia are so important, the boundaries have been drawn in this area. Such a decision is somewhat unsatisfactory, but any definite placement of a transition zone into a regional division is always arbitrary.

Comparisons and Discussion

The average pattern of vertebrate geography¹ has been subjected to only minor alterations since the proposals of Wallace and Selater. The Australian region (New Guinea, Australia, and Tasmania) is considered to be a homogeneous faunal unit (Darlington, 1957, pp. 449–452) to which New Zealand and the Pacific Islands form an "impoverished . . . appendage" (Schmidt, 1954, p. 327) or a separate "fringing pattern" (Darlington, 1957, p. 452). I am unorthodox in including New Guinea, coastal Queensland, and the Admiralty, Bismarck, and Solomon Islands in the Palaeo-Oriental region; in uniting Australia, Tasmania, New Zealand, and New Caledonia into one faunal division; and in recognizing a distinctive "Polynesian" fauna.

¹ See Darlington (1957, pp. 420–423) for a discussion of the meaning of faunal regions to vertebrate distribution.

The Australian faunas of New Guinea is very convincing for mammals and birds (see Mayr, 1944, 1953b) but not for land snails. If coastal Queensland is eliminated, New Guinea has practically no Australian land snail taxa, and nearly all the families and genera can be traced to Malayan origins (see Hedley, 1895b). Paul H. Fischer (1880-87) (see fig. 30), A. H. Cooke (1895) (see fig. 31), and P.-H. Fischer (1950) (see fig. 32) all recognized that the mollusk fauna of New Guinea is quite different from that of Australia. Their failure to recognize its Indonesian aspect is perhaps partially due to the influence of vertebrate geography, although their work was done prior¹ to the anatomical studies of Pilsbry, Hedley, H. B. Baker, Watson, and Thiele. The classification developed through these anatomical studies affords the primary evidence for denying the Australian nature of the New Guinea snail fauna.

The faunal similarity of New Caledonia and New Zealand was recognized by Hedley (1899, p. 402) and Germain (1934, pp. 145-146). It is based on the radiation of endodontids and paryphantids. Generic affinities are probably few, but the general faunas of the snail fauna is the same. As has been emphasized above, Australia has an intrusion of more recent elements. This also applies to other phyla. The land mammals of Australia are absent from New Zealand, and the rich and varied Australian bird and herpetofauna contrast strongly with those of New Zealand. The importance of these differences will be considered in more detail later in this paper.

The concept of the "Polynesian" region, with a distinct snail fauna, dates from Pilsbry (1900b, p. 573) who stated: "Far from being a faunal dependency of the Australian or Oriental regions, Polynesia has every appearance of being a region which started with a fauna long antedating the present Australian and Oriental faunas, developing along its own lines, retaining old types because they did not come into competition with the higher groups developed on the greater and less isolated continents." The Partulidae, Amastridae, Tornatellinidae, and Pupillidae are at the very base of the land snail phyletic tree (see fig. 11). The Orthurethra are probably the living group nearest to the stylommatophoran ancestor, and Pilsbry (1916, p. 430) considered their relationship to the Sigmurethra the same as that of the monotremes to the placental mammals. The occurrence of tornatellinids on the Mascarene islands only emphasizes the age of the group, since their land snail fauna is only a little less antique than that of the Pacific islands. Among the Sigmurethra—the most

¹ P.-H. Fischer (1950) is virtually a copy of Paul H. Fischer (1880-87).

advanced land snails—it is only the more primitive Aulacopoda which reaches the Pacific islands. The Microcystinae is endemic and is the most primitive helicarionid subfamily. The most primitive zonitid subfamily, the Trochomorphinae, reaches only *part* of the Pacific, while the most primitive aulacopod family, the Endodontidae, has several generic units on the islands. Holopod snails, except for introduced species, are not found in Micronesia or Polynesia.

Some other zoogeographic divisions of the Pacific are reproduced here. Those for insects (fig. 33; Holdhaus, 1934, pp. 209–210), birds (fig. 34; Mayr, 1940a, p. 193, and 1944), and general zoogeography (fig. 35; Schilder, 1956, p. 86, fig. 38) all have New Guinea as part of the Australian region. A later study on the insects (fig. 36; Gressitt, 1956, p. 13) placed New Guinea and “Polynesia” in the “Oriental” or “Malayan” region.

The strong “Malayan” affinities of New Guinean plants have long been recognized by botanists (see Hayek, 1926; Guillaumin, 1926, 1934b, p. 263; Lam, 1934, p. 141; and Good, 1953, p. 30), and most phytogeographic schemes place New Guinea in the “Malayan” floral region (fig. 37, after Good, 1953, and fig. 38, after Hayek, 1926). Indeed, the divisions proposed for land snails show more resemblance to the botanical regions than to those proposed for other animal phyla.

Mayr (1953b) discussed the possible reasons for the different distributions of plants on one hand and birds and mammals on the other. To his two cited reasons—dispersal facilities and evolutionary rates—I would add a third, the time of dispersal. This has already been suggested by Burkill (*in* Scrivenor, et al., 1943, p. 138): “It is very interesting that the Mammalian and Avian views should be so unbotanical. Mammals and birds are late of evolution. Many forms of life had taken advantage of land bridges favourable early but broken down before mammals came to them; and it was on mammals and birds that so much of this geography was planned. If we seek to define Regions and Subregions on mammals and birds overmuch we evaluate the powers of barriers of the last part alone of the earth’s history. It has been claimed that it is right to do so. Then the Regions and Subregions are likely to lack interest among those who study older families.”

Ideally, biogeographic schemes are based on a consideration of the entire biota. Practically, we have angiosperm phytogeography or vertebrate zoogeography, with other organisms either ignored or assumed to conform with the angiosperms or vertebrates when their classification is “better known.” Organisms differ in means, rapid-

ity, and time of dispersal; time and place of initial adaptive radiations; and degree of dependence on their physical environment. All these factors, plus incomplete knowledge of invertebrate and non-angiosperm taxonomy, combine to prevent recognition of true "biogeographic areas." The most we can do is to recognize that differences in present distributions are the result of historical perspective and that the factors determining the present distribution of one group may have little or no bearing on the past history of another.

The faunal divisions proposed above have been based on land snails and show little correlation with the distribution patterns of the vertebrates. Darlington (1957, pp. 420-423) made a strong plea to fit the distribution of other taxa into the average geographical pattern of the vertebrates. I have not done so. Each particular class or phylum should have its distribution presented on its own merits. As the data from the non-vertebrates and non-angiosperms accumulate over the years, an eventual synthesis of *biogeography*, rather than the present vertebrate or angiosperm geography, can be prepared. In the meantime, I prefer to let the land snail pattern stand by itself, rather than twist it into the framework of classical vertebrate geography.

The present distribution of any taxon may be treated separately, but the history of a biota must encompass that of all living organisms found in the area. The "static zoogeography" above is based on land snails, but in the "dynamic zoogeography" below, I have attempted to synthesize data from vertebrates, and, to a limited extent, from entomology and botany as well as from land snails.

ORIGIN OF THE NEW HEBRIDEAN FAUNA

Several times mention has been made of the "oceanic" nature of the vertebrate fauna of the New Hebrides. Before trying to place the New Hebridean fauna in a historical perspective, a brief summary of the Melanesian and New Zealand vertebrate fauna will provide essential data for the historical speculations.

Vertebrate Fauna of Melanesia and New Zealand

FRESH-WATER FISHES

Myers (1951) recognized several types of fresh-water fishes, based on their degree of toleration of salinity. The "primary fresh-water fish" (those completely intolerant of salt water) are not found east of Bali. The fresh-water fishes of the New Hebrides (J. R. Baker,

1929, p. 99), New Caledonia (Darlington, 1957, p. 525), and New Zealand (Myers, 1951, p. 15) are all species that can cross salt-water filter zones between fresh-water streams. The few relict fresh-water fishes of Australia do not contradict the belief (Myers, 1951, p. 18) that the Australian region has had no Cenozoic land connections with Asia.

MAMMALS

The only New Hebridean mammals are rats, a feral pig, and several bats (see J. R. Baker, 1928, and Sanborn and Nicholson, 1950). Some of the New Hebridean bats are endemic; others are also found in the Solomons and New Caledonia. The rats and pigs of the New Hebrides were introduced by man. New Caledonia and New Zealand agree with the New Hebrides in having only native bats and introduced mammals. In sharp contrast is the famous marsupial fauna of Australia and New Guinea. The northern Solomon Islands have a few mammals, three rodent genera (*Uromys*, *Solomys*, and *Melomys*) and a marsupial (*Phalanger orientalis*), but no other islands of the Pacific have native mammals (see Laurie and Hill, 1954).

REPTILES AND AMPHIBIANS

New Hebrides.—The herpetofauna of the New Hebrides is more extensive (see Roux, 1913; J. R. Baker, 1928; and Burt and Burt, 1932). No amphibians have been previously reported from the New Hebrides, but Kuntz found an Australian tree frog, *Hyla aurea aurea*, on Espiritu Santo. Since Speiser did not find this frog in 1911 (Roux, 1913), it is probably a very recent introduction and provides an intriguing corollary to the suggested snail "imports and exports" between Australia and the New Hebrides (see p. 12, no. 1, this volume). Of the 21 New Hebridean reptiles (see Table XVIII), 14 also live in New Guinea; 13 in the Fijis; 9 in the Loyalty Islands; and 5 in New Caledonia. Only two species and one subspecies are endemic. Six Solomon Island species reach the Santa Cruz Islands, but not the New Hebrides. The fauna moving from New Guinea shows a regular progression in the reduction of number of species represented. All of the New Hebridean reptiles were probably derived by "sweepstakes" dispersal over the present ocean gaps. The faunal attenuation of New Hebridean species between the Loyalty Islands (9) and New Caledonia (5) suggests the New Hebridean to New Caledonian passage offered by storms, winds, and ocean currents (see p. 19, no. 1, this volume).

Of the reptiles, the Hydrophiidae are sea snakes and the crocodile and boid snakes are good swimmers (also *Ahaetulla* of the Santa Cruz Islands), while the geckos have water-resistant eggs with long incubation periods. The eggs are often laid on logs. An example of living gecko eggs found on a drifted tree trunk is reported by Kew (1893, p. 138). The mechanisms for passive dispersal utilized by skinks are unknown, but their wide distribution suggests that these means are very effective. In recent times, of course, the factor of dispersal

Table XVIII.—New Hebridean Reptiles

Species	Distribution						
	NG ¹	SI	SC	NH	LI	NC	F
Geckonidae							
<i>Gymnodactylus pelagicus</i>	x	x	x	x	x	x	x
<i>Gehyra oceanica</i>	x	x	x	x	x	x	x
<i>Peropus mutilata</i>	x			x			x
<i>Lepidodactylus lugubris</i>	x	x	x	x	x	x	x
<i>Gecko vittatus</i>	x	x	x				
<i>Lepidodactylus guppyi</i>	x	x	x				
<i>Perochirus guentheri</i>				x			
Scincidae							
<i>Cryptoblepharus boutonii peronii</i>	x			x	x	x	x
<i>Dasia smaragdina perviridis</i>	x	x	x				
<i>Emoia cyanogaster</i>	x	x	x	x			
<i>E. cyanura</i>	x	x	x	x	x		x
<i>E. nigra</i> (= <i>speiseri</i>)		x	x	x			x
<i>E. atrocostatum</i>	x		x	x			
<i>E. samoensis</i>			x	x	x		x
<i>E. sanfordi</i>		x	x	x			
<i>E. werneri</i>	x	x		x			
<i>E. nigromarginatum</i>				x			
<i>Leiopisma noctua</i>	x	x		x			
<i>L. a. austro-caledonica</i>				x	x	x	
<i>L. a. metallica</i>				x			
<i>Riopa albofasciata</i>	x	x	x				
Boidae							
<i>Engyurus australis</i>	x	x	x	x	x		x
<i>E. bibroni</i>	x	x		x	x		x
<i>E. carinatus</i>	x	x	x				
Colubridae							
<i>Ahaetulla calligaster</i>	x	x	x				
Hydrophiidae							
<i>Laticauda colubrina</i>	x	x		x			x
<i>L. laticauda</i>	x		x				x
Crocodylidae							
<i>Crocodylus porosus</i>	x	x	x	x			x

¹ NG (New Guinea), SI (Solomon Islands), SC (Santa Cruz Islands), NH (New Hebrides), LI (Loyalty Islands), NC (New Caledonia), F (Fiji).

by man is undoubtedly important. The New Hebrides, then, have only reptiles which could easily have been derived via overseas drift. Several species reached the Santa Cruz Islands from the Solomons, but not the New Hebrides. The similar New Hebrides-Loyalty Islands-New Caledonia attenuation also points towards overseas dispersal.

Solomon Islands.—Consideration of the reptiles found on some other islands does not present so clear a picture of passive dispersal. The Solomon Islands have endemic frogs belonging to the genera *Rana*, *Palmatorappia*, *Batrachylodes*, *Ceratobatrachus*, *Discodeles*, *Hyla*, *Platymantis*, and *Cornufer* (see Brown, 1952). *Palmatorappia*, *Batrachylodes*, and *Ceratobatrachus* are endemic genera, while *Discodeles* is found also in the Bismarck and Admiralty Islands. With the possible exception of *Batrachylodes*, all these endemic genera are closely related to the *Cornufer-Platymantis* stock (Brown, 1952, p. 11) and may represent a single ancestral stock. Besides the amphibians, the Solomons have several snakes (*Chondropython*, *Nardoana*, *Boiga*, *Stegonotus*, *Denisonia*, *Micropechis*, *Typhlops*) and lizards (*Corucia*, *Sphenomorphus*, *Tribolonotus*, *Gonyocephalus*, and *Varanus*) not found in the Santa Cruz and New Hebrides (see Barbour, 1921; Burt and Burt, 1932, pp. 478, 486-492; and Kinghorn, 1928). The much more extensive herpetofauna of the Solomons is paralleled by the more extensive land snail fauna (see p. 297).

Fiji Islands.—The Fijis have many Solomon Island elements, but most important for this study are the endemic frogs of the genera *Cornufer* and *Platymantis* (see Barbour, 1923, and Brown and Myers, 1949), a snake genus *Ogmodon*, and an iguanid lizard, *Brachylophus*. Darlington (1948, p. 20) suggested that the Fijian frogs may have been introduced, but their status is still uncertain. The iguanid lizard, *Brachylophus*, is very important. The only other Old World iguanids are found in Madagascar; otherwise the family is New World in distribution.

New Caledonia.—New Caledonia has no native amphibians, but Roux (1913) placed some of the lizards (skinks and geckos) in endemic genera and subgenera. A snake, *Typhlops willeyi*, has been reported from the Loyalty Islands, but Darlington (1957, pp. 180, 525) follows Mertens in considering the records to be erroneous or based on introduced material. I was unable to find any authoritative review of the validity of Roux's genera, so the importance of the New Caledonian lizard radiation is unknown. The groups present, however, suggest overseas dispersal.

New Zealand.—The herpetofauna is limited but extremely interesting. Three endemic *ovoviparous* geckos (*Hoplodactylus*, *Heteropholis*, and *Naultinus*), several skinks (*Leiopisma*), and the rhynchocephalian *Sphenodon* are the only reptiles. Two or three species of *Leiopelma* are the only amphibians. *Sphenodon* is the only living member of the primarily Triassic order Rhynchocephalia. The Sphenodontidae are not known as fossils since the Jurassic and no fossil rhynchocephalians have been found in strata later than the lower Eocene (Beaufort, 1951, p. 165). *Leiopelma* is related to *Ascapus* from the northwestern United States. Although these two genera are specialized in habitat, their structure places them as the most generalized anurans. Probably they are related to the discoglossid frogs but form a distinct family (Ritland, 1955, pp. 279–282). The lizards have many primitive features, but their affinities are uncertain. McCann (1955) reviewed the species of New Zealand lizards but did not consider supra generic classification.

Darlington (1957, pp. 526–527) recognized the phyletic antiquity of the New Zealand herpetofauna, but did not feel that its fossil age should be taken to mean that it has been in New Zealand that long.

Summary.—New Zealand and Fiji have important relict taxa, New Caledonia and the New Hebrides a more modern “waif fauna,” and the Solomons a fairly extensive representation of genera and families which do not reach the other Pacific Islands. George Gaylord Simpson (1956) considered the Solomons “continental,” but Darlington (1957, p. 509) suggested that the fauna is of “overseas” origin. The very few relict vertebrates of Fiji and New Zealand are, *by themselves*, not enough evidence to assume continental origins for these islands. The much more extensive Australian reptile and amphibian assemblage is evidence of the relatively passable filter zone between Asia and Australia which existed during the Tertiary.

BIRDS

Mayr (1940a,b) analyzed the bird fauna of the New Hebrides. Perhaps half of the 53 species of land birds range over much of the Pacific. Two endemic genera¹ and four other endemic species (of Papuan affinities) form the only special elements. Distribution within the islands is irregular (Mayr, 1940b, p. 211), and the bird fauna does not seem to be indicative of any great age or continental connection. The Banks Islands have the same fauna as the rest of

¹ *Cichlornis*, which may be related to the New Caledonian *Megalurulus*, and *Neolalage*, which is related to the Papuan *Monarcha*.

the New Hebrides, but the Santa Cruz Islands present a "blending" of Solomon Island, Fijian, and New Hebridean taxa (Mayr, 1940b, pp. 211-212).

New Caledonia has the remarkable kagu (*Rhynochetos*) and four endemic genera, two of "Australian," two of "Papuan" origin. The fauna is almost equally Australian and Papuan in affinity (Mayr, 1940b, pp. 209-210) and does not indicate any great age.

New Zealand has a remarkable fauna of flightless birds (moas, kiwis, rails) and some endemic flying birds as well as taxa of very recent overseas origin (Darlington, 1957, pp. 526-527). Many are related to Australian taxa.

Australia has many birds from the Oriental region but contains the largest proportion of purely endemic birds of any continental area except South America (Darlington, 1957, p. 451).

SUMMARY

The New Hebrides have an "oceanic" vertebrate fauna. Less than 10 per cent of the birds and reptiles represent endemic species (compared with 79.1 per cent of the land snail species). The most important vertebrate species of the Pacific Islands, from the standpoint of zoogeography, are the relict *Brachylophus* of Fiji, and *Sphenodon* and *Leiopelma* in New Zealand.

Faunal Elements of the New Hebridean Land Snails

The tables, distribution maps, and faunal comparisons given above serve to emphasize the complex nature of the New Hebridean fauna. Perhaps five relatively distinct faunal elements can be recognized and the land snails grouped as follows:

1. Southern Relict taxa: *Placostylus*, *Diplomorpha*, *Aneitea*, and *Phrixgnathus* (13 species).
2. Pacific Island taxa: (a) "inner fringe," *Gonatoraphe*, *Hebridelos*, and *Dendrotrachus* (6 species); and (b) "oceanian," *Partula*, *Omphalotropis* (*Lyrotropis*), *Lamprocystis*, *Diastole*, and possibly *Mocella* (12 species); total 18 species.
3. Palaeo-Oriental taxa: (a) "terminal Indonesian," *Pupina*, *Conibycus*, *Macrocyclus*, *Wilhelminaia*, *Trochomorpha*, probably *Palaina* and *Discocharopa* (11 species); (b) "Papuan," *Ouagapia*, *Orpiella*, *Papusuccinea* (3 species); total 14 species.

4. "Coral Atoll" taxa dispersed by natives: the species on p. 210, no. 1, this volume, and possibly *Pleuropoma articulata* (Pfeiffer) and *Omphalotropis setocincta* Ancey (10 species).
5. "Tropical Tramps" introduced by the Caucasians (see p. 209,) no. 1, this volume (6 species).

The position of few taxa is problematic. *Draparnaudia* (2 species) may be a tornatellinid (Pacific Island) or camaenid (Palaeo-Oriental) (see p. 121, no. 1, this volume); *Reticharopa* (5 species) may be Palaeo-Oriental or a Southern Relict; and the endemic *Pleuropoma* may be Palaeo-Oriental or Pacific Island. On the basis of our present knowledge of speciation, the three endemic elements form relatively equal portions of the fauna. Allocation of the several uncertain taxa could either maintain the status quo or shift it heavily to the Palaeo-Oriental or Pacific Island faunas. Adequate collections in the New Hebrides may completely change the "faunal balance."

The problems of age, origin, and spread of the Australian snail fauna were considered by Hedley (1899), and C. M. Cooke (1926, p. 2278) postulated four colonizing waves for Polynesia. Ideas presented by both men are found in altered form below and the basis for the hypothesis presented here is contained in their studies. Yet the synthesis differs from the parts and little below is directly quoted from these papers or those of Pilsbry.

Direction of Derivation

With the exception of the Bulimulidae, Paryphantidae, and Athoracophoridae, all the New Hebridean land snails can be directly derived from taxa which are now living in the Indo-Australian archipelago or, because of their arc-like distribution around New Guinea, were obviously formerly found there.¹ The Paryphantidae have a disjunctive distribution in South Africa, Australia, and Melanesia, with a few species in Indonesia; the Bulimulidae live in southwestern Australia, Melanesia, New Zealand and Central and South America, with one dubious record (*Prestonella*) from Africa; and the Athoracophoridae are restricted to the New Guinea-New Zealand axis.

The problem of discontinuous distributions in the southern hemisphere has long puzzled zoogeographers. The faunal affinities between South Africa, Australia, New Zealand, and South America (plus sub-Antarctic islands) led many authorities to postulate Antarctic origins, or at least migrations, for many phyla. At the begin-

¹ The few Nearctic elements in the Pacific snail fauna are discussed by H. B. Baker (1941, 1958, pp. 145-146).

ning of this century this theory was highly favored as an explanation of the present distribution of marsupials. Subsequent studies (summarized by G. G. Simpson, 1940) showed that the similarities between South American and Australian marsupials are caused by common derivation from the Holarctic rather than faunal interchange through Antarctica. As far as vertebrate zoogeography is concerned, Matthews' theory of origin in the Holarctic land mass followed by spread into the southern hemisphere stands almost unchallenged (see Darlington, 1957, pp. 602-606).

In phyla of much greater age than the mammals, many extremely closely related organisms are found in the southern lands. Many botanists (see Skottsberg, 1953) and entomologists and several malacologists (Hedley, 1899; Ortmann, 1921; Grimpe and Hoffmann, 1925a; Germain, 1934) have postulated a faunal interchange between the southern lands and Antarctica. Antarctica once had a much warmer climate than it has now. The finding of fossil plants such as *Acmopyle*¹ and *Araucaria* in Antarctic Tertiary coal beds (Skottsberg, 1953, p. 96) certainly adds credence to belief in the Antarctic route. I am not competent to evaluate the botanical or entomological evidence for or against such an interpretation and shall make no effort to do so. The eventual disposition of the Antarctic migration route will depend on more thorough explorations of the fossil beds of Antarctica.

LAND SNAILS

In regard to the land mollusks, however, certain conclusions can be drawn. The Paryphantidae are considered to be ancestral to the Streptaxidae, a family of more northern distribution. This relationship would make northern origin and dispersal more probable than southern ones. I have demonstrated that the probable phylogenetic sequence in the Athoracophoridae suggests a northern rather than a southern origin (see Grimpe and Hoffmann, 1925a, for the opposite view). The phylogeny of the South American Bulimulidae is uncertain, and the proposed sequence in *Placostylus* is only tentative. Nevertheless, fewer problems are encountered in explaining the distribution of *Placostylus* if a spread from north to south rather than the reverse is postulated (see p. 327). The only other major molluscan taxon of southern distribution, the Acavacea, has been shown by Watson (*in* Connolly, 1915) and Germain (1925) to be derived from the Holarctic land areas.

¹ Found living only in New Caledonia and Fiji.

On the basis of present phylogenetic interpretations all these families have the more primitive species and genera farther south, and the more advanced farther north.

I am thus concluding that there are no land snails present in the Austro-Zealandic fauna which did not originally come from the Indo-Australian archipelago.

FRESH-WATER CLAMS OF THE PACIFIC REGION

Many people have noted the similarities between the fresh-water mussels of Australia, New Zealand and South America. Indeed, they were at one time placed in the same genus. Recent workers (Ortmann, 1921, and McMichael and Hiscock, 1958) recognized a southern family, Mutelidae, with two subfamilies, the Mutelinae and the Hyriinae. Mutelinae are found in Central America, northern South America, and possibly Africa; the Hyriinae are distributed over most of South America (but primarily in the southern half), Australia, New Zealand, New Guinea, and the Solomon Islands. Ortmann (1921, p. 454) suggested that the Australian unionids might contain two elements, an older one related to South America and a younger one derived from southeastern Asia. Iredale (1943b) did not accept these conclusions and created many new families and genera for the Australian mussels. McMichael and Hiscock (1958) referred two New Guinea mussels to the Unionidae and placed the vast majority of the Australian, New Zealand, New Guinea, and Solomon Island species in four closely related subfamilies of the Mutelidae.

Haas (personal communication), in reviewing the Unionacea for the *Treatise of Invertebrate Paleontology*, concurred with Ortmann by placing the New Guinea, Queensland, and Solomon Island genera (*Virgus*, *Leiovirgus*, and *Cucumerunio*)¹ in the subfamily Unioninae (a Holarctic, African, and Oriental taxon) with the remaining species in the subfamily Hyriinae. This is in direct conflict with McMichael (1956) and McMichael and Hiscock (1958), who place all the genera in the Mutelidae. Reproductive habits are not worked out for the Australian forms, and resolution of the differences between Haas and McMichael is impossible.

The absence of primary fresh-water fish from Australia and New Zealand has undoubtedly affected the unionid fauna, and study of

¹ McMichael (1958) referred one New Zealand species to the genus *Cucumerunio*. Haas (personal communication) has examined paratypes of this species and believes that it is a local derivative from New Zealand *Hyridella* and that it is only convergent to the Australian *Cucumerunio*.

the reproductive habits will have an important bearing on the determination of their true relationships.

The significant facts for this study are the presence of fossil Hyriinae in the Cretaceous of Patagonia, and fossil Mutelinae in the Cretaceous of Brazil (*teste* von Ihering). These data indicate that the South American taxa had reached their *present* distribution by the Cretaceous. Not enough information is available about the unionids of the Southern Hemisphere to draw detailed conclusions as to their affinities and geographic origin. On the basis of the fossil evidence and family boundaries outlined by Ortmann, they can be correlated with the probable land snail distribution and also derived from the north. In the absence of conflicting evidence other than Iredale's taxonomic obscurantisms, they are here considered to be part of the same general pattern.

Pattern of Austral-New Zealand Land Snail Origins

Assuming northern derivation for the land snails and unionids, can we delineate definite waves of colonization, or is the fauna completely mixed? If the Austro-Zealandic snail fauna is examined as a unit, four large "waves" of immigrants can be recognized. The Melanesian fauna is complicated by several subsidiary factors, and discussion of these special aspects will be deferred until after the general pattern has been traced.

The fauna of southern Australia and New Zealand is dominated by paryphantids, endodontids, bulimulids and hyrine mussels. New Zealand differs in having Athoracophoridae and Cyclophoracea; southeast Australia and Tasmania have Acavacea and only one bulimulid; and southwest Australia has no paryphantids.

This distribution is most simply explained by postulating a single "basic" fauna of primitive Paryphantidae, Endodontidae, Bulimulidae, Athoracophoridae(?), and Hyriinae that occupied all of southern Australia, Tasmania, and New Zealand. This assemblage has been subsequently modified by climatic changes and the competition of the three succeeding waves of land snails which reached parts of Australia. Present knowledge of the fossil history and phylogeny of these basic elements does not permit any speculation about the relative age of these taxa or their sequence of arrival. McMichael (1957) reported fossil fresh-water clams from the Upper Cretaceous of New Zealand and as early as the Triassic and Jurassic of Australia, so that these original elements are of great antiquity.

No Athoracophoridae or Paryphantidae are presently found in southwest Australia. The comparatively dry climate of this region may be the excluding factor and, in the past, they may have lived there. Whether the New South Wales athoracophorid (Iredale, 1938, pp. 121-122) is a relict or part of a later immigration is unknown.

New Zealand seems to have remained effectively isolated from subsequent molluscan colonization and southwestern Australia only slightly less so. Southeast Australia and Tasmania received at least one other definite colonization wave, consisting of the Mesurethran family group Acavacea, which did not reach New Caledonia, and several advanced paryphantids and endodontids, which did. The Acavacea probably displaced the bulimulids, which remain as only a single species of *Bothriembryon* in Tasmania. Since then, southeastern Australia appears to have been almost as fully isolated as southwestern Australia.

The isolating mechanisms for the three areas are different. In New Zealand there was the present water barrier, in southwestern Australia a combination of a shallow sea and the Central Desert, and in southeastern Australia and Tasmania the mountains of the Great Dividing Range (see Hesse, Allee and Schmidt, 1951, p. 77). Land masses evidently are less effective barriers to terrestrial Mollusca than extensive water gaps, since southwestern and southeastern Australia and Tasmania have received a very few modern elements (Camaenidae, Limacacea) which filtered through the land barriers.

The third distributional wave to Australia would include the endemic Australian camaenids and possibly the unionids that are more related to Asiatic than South American species.

The fourth and last colonizing wave is the "Papuan" fauna of coastal Queensland and northern New South Wales. This assemblage includes the *Thersites* and *Hadra* endemics, a few "*Papuina*" and "*Chloritis*" in the Camaenidae, *Pupina*, Cyclophoridae, rathouisiid slugs, and helicarionids.

Time of Origin

Assigning tentative dates to these four waves is difficult because of the lack of direct geologic and paleontologic evidence, especially in Australia. The dating must be based on analogy from fossils in South America and the Holarctic; on negative evidence from the distribution of advanced snails and vertebrates; and on backward projection of evolutionary rates in land mollusks. The errors inher-

ent in such procedures are large, but in absence of direct evidence no other course is possible.

Until the Cretaceous and Paleocene, non-marine molluscan fossils are practically non-existent. The geographic locations of certain Cretaceous to Eocene land mollusks are significant in respect to the Australian fauna. Acavacea, Bulimulidae, and Hyriinae are *present* in the Cretaceous and Eocene of Patagonia, but are *absent* in North America and Europe (except for an advanced bulimulid, *Grangerella*). Fossil camaenids are known from the Cretaceous of North America and the Eocene of Europe (where they have been replaced by advanced helicoids). *The absence of Bulimulidae and Acavacea from deposits in the Northern Hemisphere would tend to suggest that these families had been replaced by the camaenids (which were present in the northern areas) before the Paleocene and Eocene strata were deposited.* The South American fossil occurrences indicate that the southern disjunctive range of the Acavacea, Bulimulidae, and Hyriinae had been established before the Eocene.

Camaenids were well differentiated and widely distributed in the Cretaceous. Their absence from southern Australia and New Zealand suggests that the barriers preventing their dispersal have been present since the Cretaceous. The basic fauna of the Austro-Zealandic region and the Acavacea must have reached this area before the start of the Cretaceous. According to Mayr (1953b, pp. 16-17), Malaya and New Guinea were connected by land in the Mesozoic, so that arrival via a "land bridge" is not impossible for these original elements. The absence of a fossil record for the Athoracophoridae and Paryphantidae is not a serious objection. Fossil slugs (Athoracophoridae) are not to be expected, and the shells of the carnivorous Paryphantidae contain few calcareous elements and thus are not apt to be preserved.

Evidence from the relict vertebrates does not contradict this hypothesis. Fossil frogs are known from the Jurassic, and the New Zealand *Leiopelma* is one of the most generalized anurans. The New Zealand lizard, *Sphenodon*, does not differ significantly from Jurassic fossils of the same family, and the origins of skinks, geckos, and iguanids go back to the Mesozoic. Whether the moas are relicts or are derived from flying ancestors of more recent arrival is inconsequential. The snails, lizards, frogs, and other primitive New Zealand relicts (Hesse, Allee and Schmidt, 1951, p. 112) all suggest that the New Zealand land fauna has been effectively isolated since Jurassic time. Oliver (1953) suggested that the New Zealand flora came via a

Cretaceous land bridge, with a few modern elements added by over-seas dispersal.

By analogy, the molluscan fauna of southern Australia would date from the same period. The spread of the second wave of mollusks, the Mesurethra, would have occurred after the barriers to New Zealand and southwestern Australia had been formed. The marsupial fauna probably came to Australia with the influx of the camaenids and Asiatic unionids. The modern birds and reptiles that now inhabit Australia can be considered "sweepstakes" winners. The date of the camaenid invasion should be placed in late Cretaceous or Paleocene to allow for the amount of differentiation present in Australia.

The fourth wave, the Queensland fauna, probably is of mid-Tertiary origin and entered across a Torres Strait filter bridge. Undoubtedly many crossings are involved.

Acceptance of the above sequence would place the family categories in the right temporal periods and allow for the generic differentiation and replacement that has occurred in Australia. The preservation in New Zealand and southern Australia of primitive generic types that are practically those of fossil relatives is the result of lack of selection pressure and competition from advanced taxa in these "refuge" zones. A Cretaceous (or earlier) immigration of the Camaenidae explains their essentially continuous distribution from southeastern Asia to the Solomon Islands, since Wallace's and Weber's lines are the result of Tertiary phenomena. Only the most advanced land snail taxa reach their distributional limits at Wallace's or Weber's lines, although many vertebrate taxa do so.

The temporal periods proposed for the "waves" of immigration are the latest consistent with geological and evolutionary data on land snails. It is very probable that the members of the "first wave" may substantially antedate the proposed Jurassic-Cretaceous spread. Because of the relative lack of pre-Tertiary land snail fossils there is no direct evidence of Mesozoic and Paleozoic distribution patterns. We can only recognize that in the South American Paleocene unionid and land snail distribution was almost the same as today. The fauna consisted of groups which had already been replaced in the northern hemisphere. The absence of molluscan faunal changes during the Tertiary equivalent to the great ones found in the mammals suggests that snails have a lesser capacity for crossing filter zones. The inability of the more modern Australian mollusks to move from the coast of Queensland down into Tasmania, although marsupials have

done so, may be partially caused by climatic factors, but with the great climatic changes known to have occurred throughout the Tertiary this failure cannot alone explain the differences between mammal and land snail distributions.

Mode of Arrival

To interpret the present land snail regions of the Pacific Islands it is necessary to explain several factors which do not apply to the other phyla of animals. The more important are:

(1) The existence of a distinctive "Polynesian" fauna composed of the land snail "monotremes."

(2) The basic faunal homogeneity of New Caledonia, New Zealand, and Australia (exclusive of Queensland and the Central Desert).

(3) The overwhelmingly "Malayan" facies of the New Guinean land snails.

(4) The absence from the Pacific region of land snail families which had Holarctic distribution in the Eocene.

It is extremely difficult, if not impossible, to explain these factors by assuming "passive dispersal" over present oceanic filter zones during the Tertiary Period. Whereas most vertebrates show a regular dispersal pattern compatible with overseas dispersal, the land snails do not. The very primitive nature of the Southern Relict and Pacific Island faunas; the phylogenetic sequences in the Placostylinae; the faunal "break" between New Caledonia and the New Hebrides; the absence of Solomon Island or Fijian taxa from the Santa Cruz Islands; and the presence of direct New Hebridean-New Zealand relationships—all are very difficult to explain if the fauna originated from passive dispersal in the Tertiary.

PACIFIC ISLAND FAUNA

Pacific Island land snails present two seemingly contradictory trends. The dominant taxa are the Orthurethra (the land snails comparable to the "monotremes" or "marsupials") and the most primitive taxa of the Aulacopoda (the Endodontidae and Microcystinae). Phylogenetically these are the oldest land snails and most of them have few continental relatives. None of the holopods are native to the Pacific, although introduced ones have flourished. The exclusion of the modern elements by the endemics thus cannot be considered an explanation for the primitive relict nature of the

snail fauna. In contrast to the nature of the fauna as a whole, there is evidence that there has been considerable gene exchange between the populations of the various archipelagos. Dr. Yoshio Kondo could discern no clear evolutionary patterns within the Partulidae, but rather a series of "centers of evolution" and considerable "reshuffling" of faunal elements. In studying the nearly endemic Microcystinae, H. B. Baker (1941, p. 358) concluded: "While, in general, their distribution and relationships conform with the theory of evolutionary divergence, certain remarkable convergences almost look as if some of the branches of their subfamily tree had inosculated and produced stocks of double origin." Relationships within the Tornatellinidae and Assimineidae appear to be equally complex, but they have not been fully interpreted at this time.

The primitive nature of the land snail fauna caused Pilsbry (1900b, 1916, 1921), C. M. Cooke (1926) and Germain (1932, 1934) to propose a Paleozoic or Mesozoic "Mid-Pacific" continent of which the high islands are fragments. Students of vertebrate zoogeography, without exception, have rejected such a hypothesis. The indications of gene exchange between populations on different archipelagos suggest that passive dispersal must have played an important role in determining the present distribution of the island snails. It is obvious that the longer the water gap, the less chance there is for passive dispersal. Recent evidence from the deep core borings at Bikini Atoll (see pp. 248, 255) suggests an explanation of the presence of primitive taxa and the absence of more modern ones.

The Bikini core drillings and the numerous guyots in the mid-Pacific indicate that there has been substantial subsidence of the Pacific Ocean floor in the Tertiary Period. Although almost none of the present high islands have been in existence for more than a fraction of the total history of the area, it is not unreasonable to suppose that there have been isolated high islands in the Pacific throughout most of the time life has existed on the earth. The geologically constant elevation and subsequent population, and the erosion and subsidence of the islands would "select" a fauna capable of being passively dispersed. I have tried to show that all the Polynesian land snails are forms whose habits present opportunities for passive dispersal by one mechanism or another, or that the forms are derivable from species which can be passively dispersed. The few "Pacific Ocean" species found in Indonesia such as tornatellinids and assimineids could thus represent introductions from "Polynesia" to Indonesia, rather than relicts in the Indonesian region of today. The method of original introduction of the fauna into Polynesia is

problematic. Whether at one period there were much more extensive land areas that allowed the introduction of the present elements and that this period was followed by one of subsidence and "rigorous selection" for passive dispersal, or whether the "Polynesian" snails had an innate capacity for utilizing passive dispersal is unknown. The exclusion of advanced taxa from the islands can be due to great water gaps that were present in the Tertiary. The addition of some Palaeo-Oriental taxa to the "inner fringe" of islands (see p. 307) may indicate more extensive land, and thus shorter water gaps in the early Tertiary. Certainly the extreme differentiation of generic units in the Palau and Caroline Islands suggests a fauna compressed into a smaller area rather than a series of introductions into a "virgin" environment—which would result in explosive speciation (as in Hawaii).

I believe that the present land snail fauna of the Pacific Islands originated in at least the early Mesozoic and has been able to survive by being passively dispersed at *very* infrequent intervals from island to island. It is not necessary to derive all the Pacific Islands from a continental mass, as did J. W. Gregory (1930), but the probability of a *greater number of islands than there are at present* cannot be ignored. Absence of relict vertebrates, higher insects, and plants from these Pacific islands does not preclude former introductions in the time of smaller gaps but their absence might have been caused by extinction during the Tertiary subsidence of the Pacific basin because the species could not adapt readily to passive dispersal.

SOUTHERN RELICT FAUNA

In regard to the Southern Relict fauna of New Caledonia, New Zealand, and Australia, a different situation exists. In these areas a regular series of faunal movements can be traced (see pp. 320-321), and in the Bulimulidae and probably in the Endodontidae and Paryphantidae also, a regular evolutionary sequence discovered. The few, but nevertheless important, land snail affinities of southwestern Australia, New Zealand, and the New Hebrides (Bulimulidae, *Mocella*); the New Caledonian-East Australian affinities (Paryphantidae, some endodontids); the comparatively few New Hebridean-New Caledonian affinities; and the completely New Hebridean nature of the Santa Cruz land snail fauna—all present difficult problems for the advocate of trans-oceanic passive dispersal to explain.

In vertebrates, land snails, and plants New Zealand has relicts of Mesozoic age but few modern elements. I would suggest that these

factors can best be explained by presumption of a former continental link between New Guinea and New Zealand which was severed not later than the Jurassic or early Cretaceous. This would account for the number of Mesozoic relicts, and the apparent continental nature (i.e., reduced degree of speciation) of their biotas. There are a few more recent additions to the biota of New Zealand, but the overwhelming "Mesozoic" aspect of the fauna contrasts greatly with the absence of "Tertiary" taxa. At the time of introduction, the New Zealand fauna was of a "balanced" nature and the "oceanic" type of speciation found in the Hawaiian Islands does not seem to have occurred. If the biota had been derived at intervals via overseas dispersal, a similar phenomenon of speciation would be expected. Acceptance of the New Zealand biota as a "balanced" one which has been long isolated from contact with the more advanced types explains the preservation of primitive types.

New Caledonia could possibly be considered an example of the same phenomenon. The fewer vertebrates and lack of close New Zealand affinities (other than on the family level), may have been caused partially by climatic factors or by severance of the New Guinea "land bridge" at a later date than that of the link to New Zealand. The time difference would not have been very great, since New Caledonia has practically no modern faunal elements except those capable of overseas dispersal.

NEW HEBRIDES

The evolutionary sequence in *Placostylus* is perhaps the most unusual result of this study. Phyletically, the New Hebrides have the oldest bulimulid elements (*Diplomorpha*), possibly not too distantly related to the southwestern Australian *Bothriembryon*. The affinities of the New Hebridean *Placostylus* to those of Lord Howe Island and New Zealand are remarkable, as is the Solomon Island-Fiji one and the intermediate nature of the New Caledonian species. A north-to-south distribution, an original movement from "Papua" to New Zealand through the New Caledonian-New Hebridean region, a second movement into New Caledonia, and a third to the Solomons and Fijis is perhaps a simpler assumption than any other alternative. Geographically, the Santa Cruz Islands are between the Solomons and Fijis, but their *Placostylus* are New Hebridean. Probably the Santa Cruz Islands were populated from the New Hebrides in the Tertiary, while the species of *Placostylus* and the iguanid lizard of Fiji may be of late Mesozoic origin.

Presence of land in the Fijian and New Hebridean regions throughout the Tertiary and late Mesozoic is without direct geologic evidence at present, but the "continental type rocks" of the Melanesian region have been known for many years and the idea of a "Melanesian continent" is not novel. If the species of *Placostylus* are the relicts of a former more extensive land area, evidently the parts of the "land mass" were submerged at different periods. Elucidation of this factor must wait for comprehensive geologic studies. The absence of relict vertebrates, except for the iguanid and the frogs(?) of Fiji, may be a factor of island size as much as extent of water gaps. Vertebrates need much larger areas than invertebrates to maintain breeding populations, and the possibility of extinction is a very real one. Assumption of a relict status for the *Placostylus* and other Southern Relict taxa is to me more satisfactory than twisting overseas dispersal to account for the many unusual features of the land snail distribution.

Obviously, the New Hebridean fauna contains many more modern elements than the Southern Relict taxa (see p. 316). Derivation of these requires no "land bridges"—only varying degrees of overseas dispersal or recent transport by humans in a few cases. For the "Pacific Island" taxa (see p. 316), winds, currents, and storms favor dispersal from Fiji to the New Hebrides. Why taxa such as the Partulidae, Microcystinae, and Trochomorphinae have been unable to bridge the gap between the New Hebrides and New Caledonia is inexplicable at the present time. Competition from the New Caledonian taxa is possible, but the latter have been replaced in continental areas by the taxa which have failed to cross the relatively narrow water gap. It becomes particularly puzzling in view of the wide "Polynesian" distribution of these taxa, much of which, if not all, must have involved the crossing of water barriers.

Of the Palaeo-Oriental taxa reaching the "inner fringe" of islands, the Poteriidae, *Hebridelos*, and *Dendrotrochus* have been replaced in the Palaeo-Oriental region, while others—Pupinidae, Diplommatinidae, Trochomorphinae, and some Helicinidae—are still found there. Dating of the arrival in the islands of these taxa is next to impossible. Those replaced on the mainland are presumably older than those which still live in the Indonesian region, but except by analogy with West Indian land snails and the application of our knowledge of the evolutionary rates in continental snails, no direct "dating" can be accomplished. Because of their subsequent replacement in the Palaeo-Oriental region, I would assume that the "inner fringe" element (p. 316) would be early Tertiary at latest, while the "termi-

nal Palaeo-Oriental" taxa would represent early to late Tertiary immigrants. The great mid-Tertiary endemism in the Greater Antilles (p. 255) and the data from the Bikini endodontids (p. 255) suggest that few major evolutionary changes have occurred in the New Hebridean fauna since the mid-Tertiary, and there probably has been little or no addition of faunal elements from then until historical times. The sunken ocean floor of the Pacific basin would provide the isolating mechanism for most of this period.

SUMMARY

The land snails of the Pacific Island fauna are relict taxa which have survived on the isolated high islands by virtue of their ability to be passively dispersed across water gaps. The absence of "modern taxa" is due to an inability to successfully utilize means of passive dispersal. In contrast to the Pacific Island fauna, the members of the Southern Relict fauna show evidence of a comparative inability to use passive dispersal and probably have been derived essentially by dry land passage and subsequently isolated by the present water gaps. The New Hebrides have a few phylogenetic relicts and many more modern elements. The "Southern Relict" taxa found in the New Hebrides may be remnants of the original fauna which passed from New Guinea to New Zealand. The modern elements have been derived by overseas dispersal at varying times during the Tertiary.

DISCUSSION

My suggestions as to the time, pattern, and mode of arrival of the Pacific land snail faunas are based on many tentative conclusions. The different distribution pattern of the land snails and, at least on continental areas, their earlier time of dispersal as compared with that of the presently dominant land vertebrates seem to be well-established. The proposals regarding the times and modes of arrival of the faunal elements are more conjectural.

I have mentioned that the distribution patterns of the land snails are similar to those of the vascular plants. Primarily, they both include New Guinea in the "Oriental" region, and there are similarities in the subdivisions of Australia. The affinities of the vascular plants of eastern Australia and Tasmania are closer than those of the land snails, but this may only reflect the lesser importance of the Great Dividing Range as a barrier to vascular plants than to land snails. In both land snails and plants there are the impoverished Eremaean

and a distinctive *southwestern* Australian biota. Probably these similarities are the result of an equally early time of dispersal for plants and land snails.

The present distribution of vertebrates seems to be mostly a product of Tertiary movements (Darlington, 1957, p. 590). In recent years evidence from the distribution of other organisms has increasingly been taken to indicate that important parts of present distribution patterns are the result of Mesozoic, or even Paleozoic, phenomena. Suessenguth (1950) derived the present Australian flora in the Jurassic or Lower Cretaceous; Oliver (1953) suggested that the New Zealand flora came by means of a Cretaceous to Eocene New Guinea land bridge; Emerson (1955) suggested a Triassic to Cretaceous origin for the Australian and New Zealand termites; and Ross (1956, pp. 169-170) considered the New Zealand caddisflies Cretaceous in origin. Ross's postulation of faunal movements of the caddisflies is in striking congruence with my own suggestions regarding land snail dispersal. The ideas were arrived at completely independently, since Ross's paper was not seen until long after submission of my thesis to the University of Michigan.

It is interesting to note that the termites of New Guinea (see Emerson, 1955, pp. 477, 503) show no endemic Australian elements; they are derived from Indo-Malaya. A similar situation in land snails resulted in my inclusion of New Guinea in the Palaeo-Oriental fauna.

Virot (1956) reviewed the vegetation types of New Caledonia and discussed the origin of the fauna and flora. The floristic affinities of the New Hebrides and New Caledonia are much closer than the malacological ones. Virot's data are taken from the studies of Sarasin and Guillaumin, and his conclusions are quite different from mine. He attempted a biogeography based on, in some cases, outmoded data, and it is not possible to present detailed criticisms of his conclusions at this time.

The hypothesis of Pacific land snail origins and dispersals presented above must be checked by careful taxonomic studies. Faunistic surveys of island groups are still needed, but monographic revisions of families and genera will be more valuable. Usually, New Zealand, Australian, or Indonesian species have been treated separately, with the result that no concept of relationships is developed in the scattered literature. Until comprehensive reviews of the Bulimulidae, Paryphantidae, Endodontidae, and Camaenidae become available, further refinement of Pacific land snail geography will be difficult if not impossible.

Specific points of interest for future investigation include the great generic differentiation in the Palau and Caroline Islands, the deep penetration of Palaeo-Oriental taxa to Samoa and Tonga, and the very striking faunal shift between the New Hebrides and New Caledonia. In tracing the dispersal patterns of different groups of land snails, it is evident that some areas have been more difficult to reach than others. The phylogenetic gap between the *Trochomorpha* of the Solomons and those of the New Hebrides is as large as the gap between the taxa of the Solomons and those of the Society Islands, yet the latter geographic gap is much greater.

Future studies will undoubtedly alter many of the phyletic and faunistic relationships postulated above, but it is hoped that at least the broad outlines of my hypothesis will withstand the scrutiny of more critical revisionary studies. In trying to summarize the phylogeny, distribution, and origins of so large and diverse a group as the land snails, I have perhaps brought a dwarf's knowledge to a giant's task. With a more detailed knowledge, a less ambitious program would have developed. Yet even the hastily sketched outline presented here may serve to stimulate others into producing the critical revisions from which a more perfect synthesis can be drawn. If this be so, then I shall feel no regret at having offered this possibly premature synopsis of Pacific land snail geography.

CONCLUSIONS

On the basis of a large collection from Espiritu Santo and material in several museums, 79 species of land and fresh-water mollusks are reported from the New Hebrides. Two of the 3 fresh-water snails are also found in New Caledonia; the other is endemic. Of the 76 land snails, 3 are inter-tidal pulmonates, 15 have been introduced by commerce or have probably been spread over the Pacific by primitive man, one is also found on New Caledonia, and 57 are endemic. Several named forms have been listed in the systematic review as species but are not accepted as "good" species in the discussion on zoogeography.

Sixteen new species and subspecies are recognized: *Aneitea robsoni santoensis*, *Succinea* (*Papusuccinea*) *kuntziana*, *Partula milleri*, *Discocharopa planulata*, *Mocella euryomphala*, *Reticharopa geddiei*, *R. stenopleura*, *R. latecosta*, *Coneuplecta* (*Conibycus*) *bicarinata*, *Dia-stole subcarinata*, *Lamprocystis mendañae*, *Orpiella* (?*Halozonites*) *retardata depressa*, *Trochomorpha* (*Hartmanitrochus*) *bakeri*, *Delos* (*Hebridelos*) *haasi*, *Ouagapia santoensis*, and *Palaina sykesi*.

Study of morphological variation in the species revealed correlations with moisture conditions and altitude. The differences were large enough for the shells to be called "subspecies," but it was considered that variations correlated with physical conditions of local areas should not be recognized as nomenclatural categories. In the islands it seems probable that ecological isolation has played an important role in speciation, and several cases of possible sympatric ecological speciation (or subspeciation) have been recognized.

Primary emphasis in this study was placed on classifying the species with their extra-limital relatives. Genera of mollusks are larger than genera of vertebrates, and detailed classifications of molluscan genera are indicated by use of subgeneric and sectional categories. During this study, six new generic units, *Reticharopa* (Pulmonata, Endodontidae), *Santotrochus* (Pulmonata, Helicarionidae), *Hartmanitrochus* (Pulmonata, Zonitidae), *Quiros* (Pulmonata, Bulimulidae), *Hebridelos* (Pulmonata, Paryphantidae), and *Lyrotropis* (Prosobranchia, Assimineidae), were proposed for New Hebridean species.

The attempts to classify the endemic species led to a survey of the distribution patterns of the land snails in the entire Pacific area. The Pacific land snails show three main types of distribution, which correspond to areas designated as the Palaeo-Oriental, Southern Relict, and Pacific Ocean regions. This distribution pattern is quite different from that shown by the vertebrates but has many similarities with that of vascular plants.

"Land snails" are composed of many phylogenetically unrelated elements, and the snails found in the Pacific Island and Southern Relict faunal areas all belong to very primitive taxa. Land snail families originated back in the Mesozoic; in South America some of the same genera found today were there in the Cretaceous. Although no direct geological evidence was available, it seems probable that the Pacific Island and Southern Relict faunas have been comparatively stable throughout the Tertiary Period and originated at least in the later part of the Mesozoic. The Pacific Island fauna has survived by being able to "island hop" from the formerly more numerous high islands to the scattered high islands of today. The water gaps in the Pacific have prevented the addition of more modern taxa during recent geological history.

The Southern Relict fauna is believed to have been derived from the Indo-Australian archipelago—not from Antarctica—by more or less "dry land" passage before the start of the Cretaceous. New Zealand and New Caledonia have been effectively isolated from fur-

ther colonizations, but Australia received additional elements—land snails and marsupials by a Cretaceous land bridge to Asia, and modern birds and reptiles by a sweepstakes route in the Tertiary.

The plants and land snails of New Guinea are Malayan rather than Australian in affinity. They were dispersed prior to the breakdown of the Asian land bridge and the creation of the filter zone which prevented the spread of the Oriental birds and mammals into New Guinea and Australia.

Snails of the Palaeo-Oriental, Southern Relict, and Pacific Island faunas are about equally represented in the New Hebrides. The Southern Relict species have more affinities with those of New Zealand than with those of New Caledonia. Possibly they are relicts of the original migration from New Guinea to New Zealand, with New Caledonia receiving its fauna from New Guinea at a slightly later date than the New Hebrides. Both the oceanic deeps and land snail distribution argue against any close affinities of the New Hebrides and New Caledonian faunas. The presence of dry land in the New Hebridean region throughout the Tertiary is without any geological evidence, but it is not improbable in view of the long geological history of some Micronesian islands.

The postulation of a Mesozoic origin for the Pacific land snail faunas contrasts with the late Tertiary origin of the vertebrate fauna of most of the islands. The presence in Fiji and New Zealand of relict vertebrates which can be considered Mesozoic, the ancient vascular plant taxa, and the primitive termite fauna all provide support for the hypothesis presented above.

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